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Ultrastructure of the Extrafloral Nectaries of *Pteridium aquilinum*

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The presence of nectaries on the stipe and frond distinguishes *Pteridium aquilinum* (L.) Kuhn from most other vascular cryptogams. The largest and most obvious nectaries are located on the stipe at the base of the lower pinnae. Nectaries on the stipe decrease in size toward the apex of the frond. The smallest nectaries are located on the abaxial surface of the frond, scattered on pinnae axes.

Described first in 1877 by Darwin, the nectaries of *Pteridium* have undergone further microscopic examination (e.g., Lloyd, 1901; Lüttge, 1961; Schremmer, 1969; Page, 1982). Lloyd (1901) noted that cells in the glandular tissue are smaller and contain more protoplasm than adjacent ground parenchyma tissue. These cells have vacuolated cytoplasm and thin cell walls. The anatomical differences noted by Lloyd have provided the basis for subsequent reviews without further elucidation. Fahn (1979a), when reviewing differences between structured and non-structured nectaries, cited the nectaries of *Pteridium* as non-structured. Structured nectaries can be identified macroscopically and their secretory cells differentiated microscopically whereas non-structured nectaries are basically unmodified tissue that secretes nectar through stomates. We find that nectaries of *Pteridium* which exude nectar through stomates can be distinguished both macroscopically and microscopically. Macroscopically, they are distinct protuberances, differing in color from the rest of the stipe and lacking trichomes. Microscopically, these nectaries are composed of layers of nectariferous tissue, distinctly specialized compared to ground parenchyma. Thus they can be defined as structured nectaries.

MATERIALS AND METHODS

Two populations of *Pteridium aquilinum* yielded the specimens in this study: one from Reston, Virginia (*Power 7734* in George Mason University Herbarium) and one from Mountain Lake Biological Field Station of the University of Virginia in Pembroke, Virginia (vouchers in Mountain Lake Herbarium). Secreting and non-secreting nectaries from stipes were excised and fixed in FAA (formalin, acetic acid, alcohol), or glutaraldehyde according to procedures outlined by Warmbrodt and Evert (1974a). Directions for dehydrating and embedding followed those in Mokotoff (1978). Tissue was embedded in Spurr's medium (Spurr, 1969). Thick (5–10 μm) sections for light microscopy were mounted on glass slides and stained with either safranin-fast green or toluidine blue; thin

sections (0.6–0.7 μm) for transmission electron microscopy (TEM) were placed on grids and viewed with a JEOL 100C microscope.

Secreting and nonsecreting nectaries were prepared for scanning electron microscopy (SEM) by fixing 5 mm sections in FAA or glutaraldehyde and dehydrating in an absolute alcohol series. Prior to fixation some nectaries were cut in two with a razor blade. They were then dried in a critical point drier. All nectaries were mounted on stubs and coated with gold-palladium, prior to viewing with either a JEOL 35C microscope or a Hitachi S530 microscope.

Results

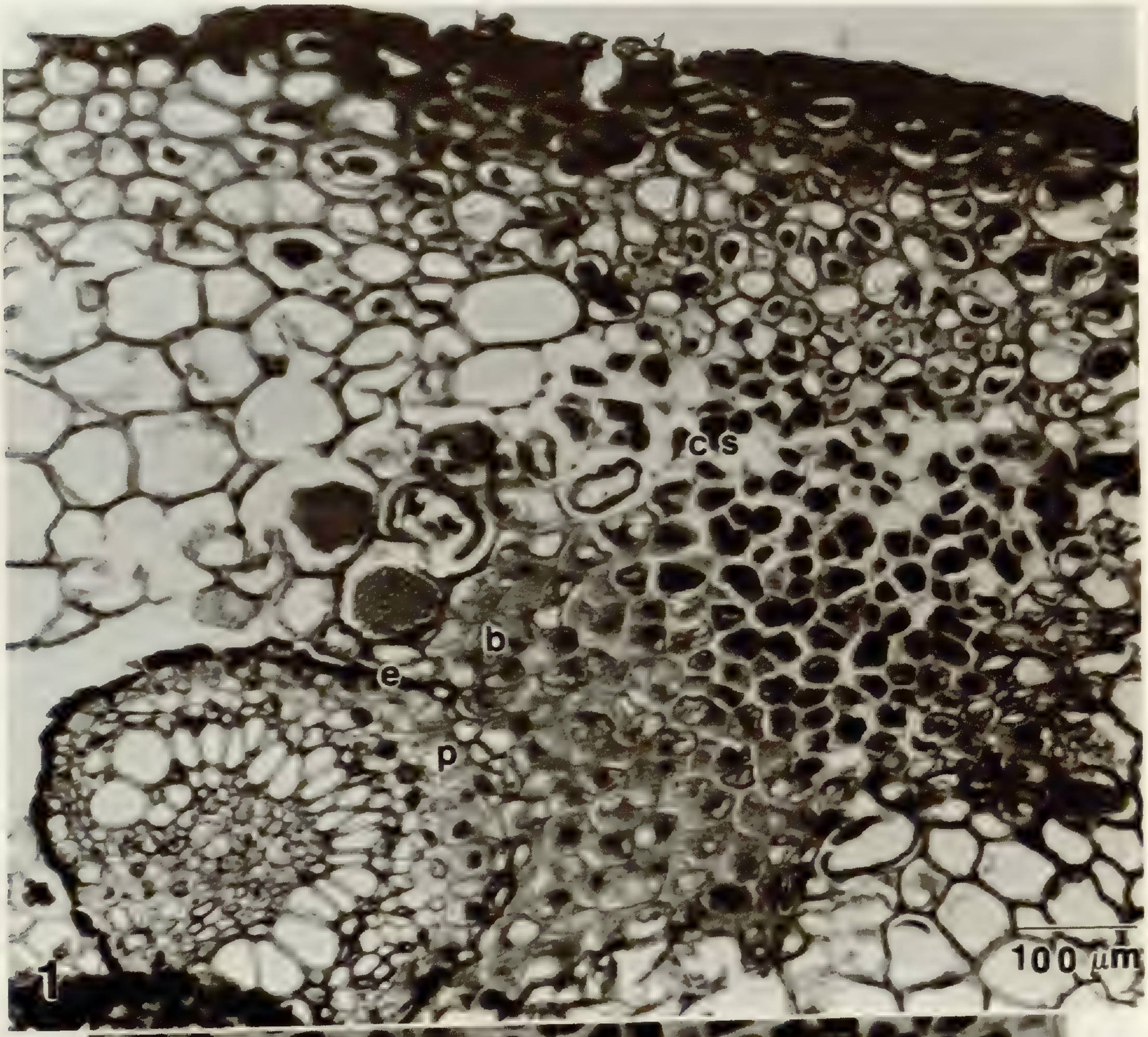
Morphologically, nectaries appear as smooth protuberances, raised 0.1–1.0 mm above the surface of the stipe. Located on the abaxial surface of the stipe at the base of each pinna or pinna pair, they are approximately 1–4 mm in diameter and vary in color from dark green (secretory) to brown (nonsecretory).

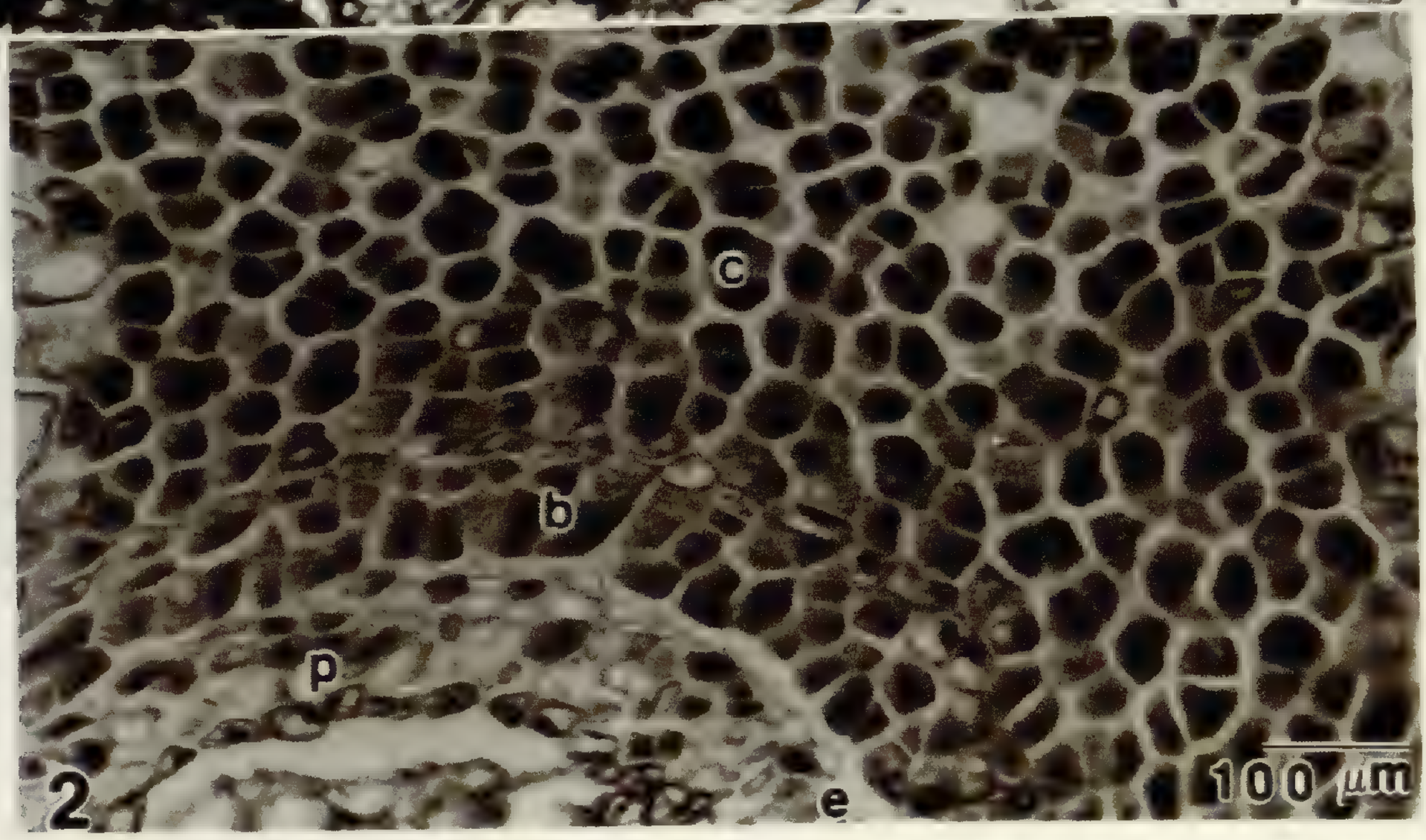
Transverse sections of the stipe show that the nectaries are distinguished from other tissues by specialized secretory parenchyma cells between the endodermis and the epidermis. The nectariferous tissue appears to be divided into three regions: a basal layer adjacent to a meristele, a broader cortical region, and an epidermal region. These combined regions measure approximately 0.3 mm from meristele to nectary surface. The tissue is 0.4 mm wide and is bordered on either side by cortical ground parenchyma cells which are large, irregular in outline and highly vacuolated. Figure 1 shows an overview of a nectary shortly after cessation of secretion; Figure 2 depicts a secretory nectary.

The basal region next to the meristele ranges from 3–7 cells wide and abuts the outer walls of the endodermis (Figs. 1 and 2). The cells are smaller than the surrounding cortical parenchyma cells and appear cuboidal. The granular cytoplasm is filled with organelles and several large vacuoles (Fig. 3).

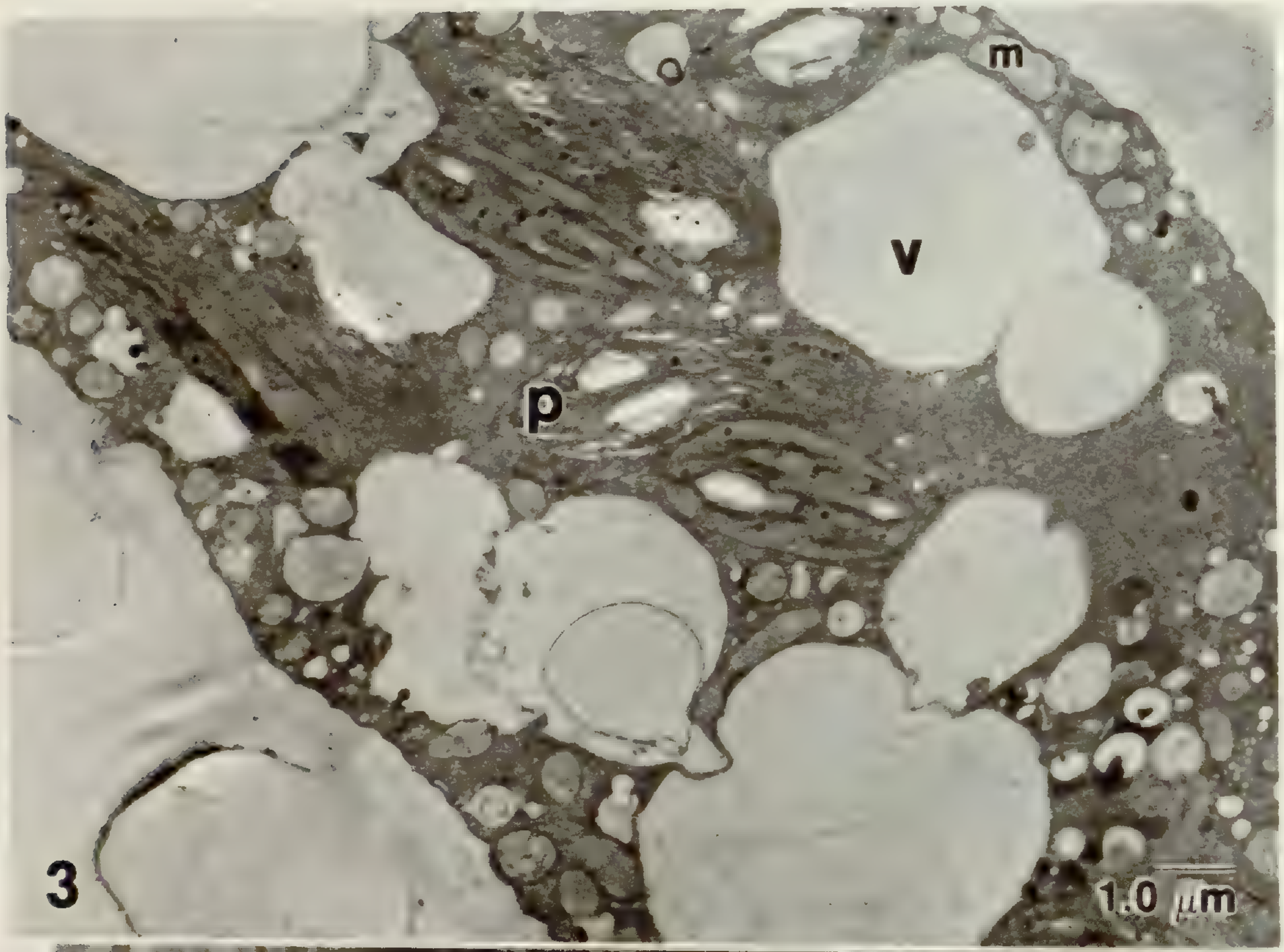
Adjacent to the basal region is an area composed of specialized parenchyma cells, the cortical secretory parenchyma. These cells are small and isodiametric, compared to the larger elongated ground parenchyma cells which compose most of the cortex and pith (Figs. 1 and 2), and contain densely staining cytoplasm filled with small vesicles but no large vacuoles. Nuclei appear large compared to the volume of the cell; each nucleus contains a nucleolus. In contrast, cytoplasm in ground parenchyma cells is more diffuse, often parietal, and hence stains very little. Nuclei occupy a smaller volume in these larger cells and are thus often excluded from the plane of section.

The cortical secretory parenchyma cells are connected by plasmodesmata which are often found within primary pit fields and simple pits if any secondary cell wall has been laid down (Fig. 4). The cells contain much endoplasmic reticulum (ER), some with enlarged cisternae, and dictyosomes. Fibrillar inclusions similar to fibrous material described by Fahn (1979b, fig. 11) can be seen outside the membrane and within the enlarged cisternae (Fig. 5). Figure 6 shows a plasmodesma between two cortical secretory parenchyma cells; this plasmodesma contains a relatively large (0.27 μm) multivesicular body and endoplasmic reticulum. A small segment of a nucleus is visible in one cell. Near the nuclear envelope is





FIGS. 1 and 2. *Pteridium* nectary anatomy. FIG. 1. Cross-section of stipe at cessation of secretion. Stomate is open, but epidermal cell walls have been thickened. Cortical secretory parenchyma (cs), basal region of parenchyma (b), the endodermis (e), and cells in the pericycle region (p) can be easily distinguished. FIG. 2. Cross-section of a secretory nectary. The cortical secretory cells (c) are distinct.



FIGS. 3 and 4. Ultrastructure of secretory nectary cells. FIG. 3. Transmission electron microscope (TEM) view of a cell characteristic of the basal region showing vacuoles (v) with some fibrillar material, plastids (p) with starch, and mitochondria (m). FIG. 4. SEM view of a cortical secretory parenchyma cell in split section showing a primary pit field. Several openings for plasmodesma can be seen (arrow).

FIG. 5. TEM of a portion of a cortical secretory cell. The vacuole is at the right. Cytoplasm contains much ER with enlarged cisternae (right arrow). Dictyosomes are near the outer membrane (left arrow) and some fibrous material (f) is outside the membrane. Some cisternae contain possible fibrous material.

a strand of endoplasmic reticulum, the cisterna of which is enlarged (Fig. 6). The other cell contains several mitochondria near the plasmodesma. Vesicles have formed adjacent to the endoplasmic reticulum. No plastids are visible in these cells.

Cortical secretory parenchyma is distinguished during its functional period by inclusion of many globules stained brilliantly red with safranin under light microscopy (Fig. 2). These globules are also visible in vascular parenchyma and basal parenchyma although they are smaller. The intercellular spaces in this cortical region anastomose into substomatal chambers.

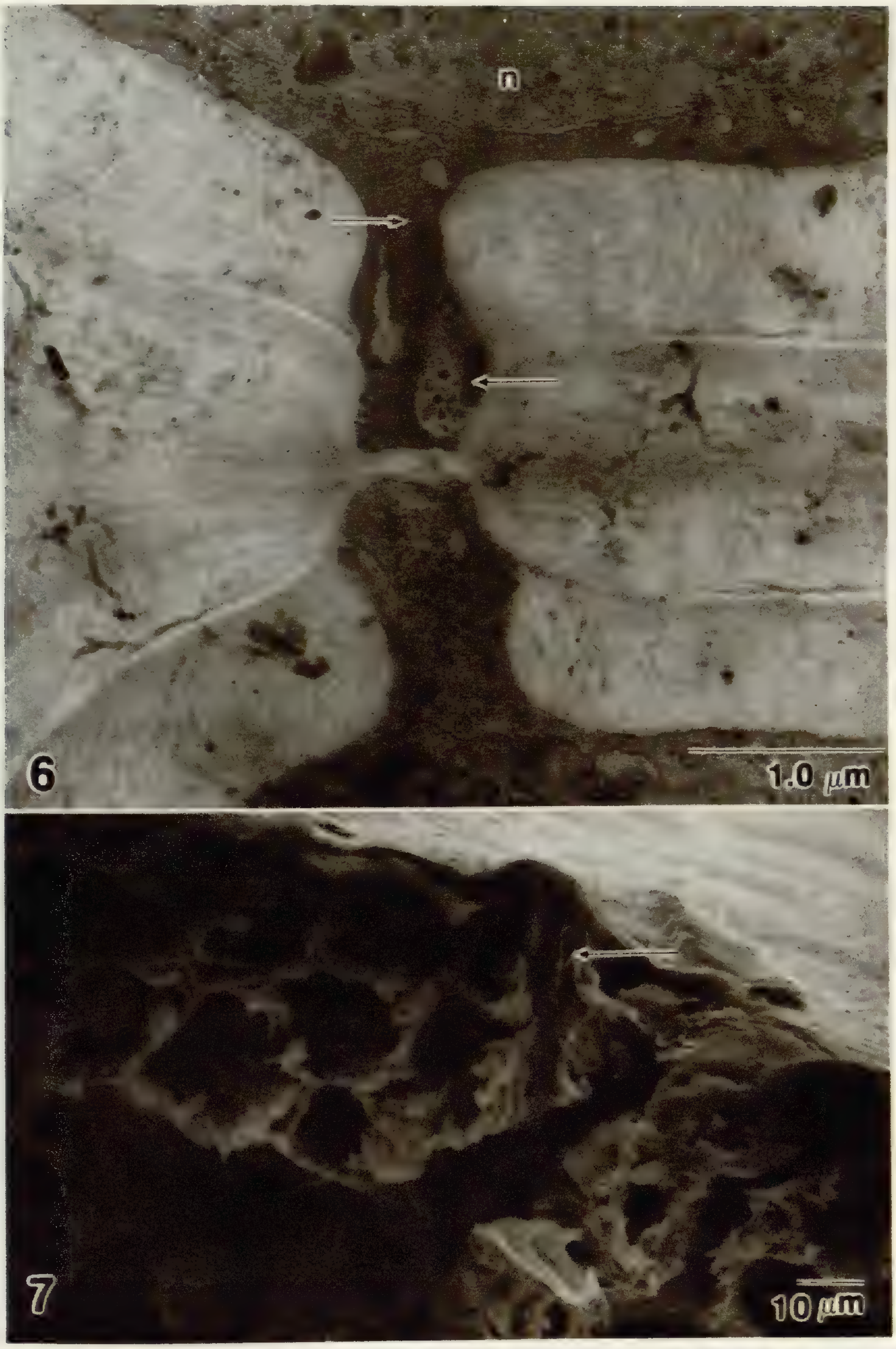
The epidermal region of the nectary is composed of 1–3 cell layers (Fig. 7). Each cell is oblong to rectangular and contains a nucleus, chloroplasts, vesicles, ER, and dictyosomes. The outer epidermal cells are covered by a thin cuticle on their outer walls (Fig. 8). The epidermal cells of the nectary are isodiametric (Fig. 9), whereas the epidermal cells of the stipe are elongated and almost linear. Stomates are much more abundant on the nectary compared to the stipe area (Fig. 9). Guard cells of the stomates are elevated above the epidermis (Figs. 1, 9, and 10). The guard cells are covered by a thin cuticle that projects into cuticular ledges (Fig. 1). The cuticle extends into the stomate and lines the substomatal chamber (Fig. 7). No subsidiary cells are present.

During the crozier stage when the nectaries are actively secreting, stomates are open and covered with globular secretions (Figs. 9 and 11). With cessation of function, the stomates become occluded (Fig. 10) and the cell walls of the epidermis become thickened and ridged.

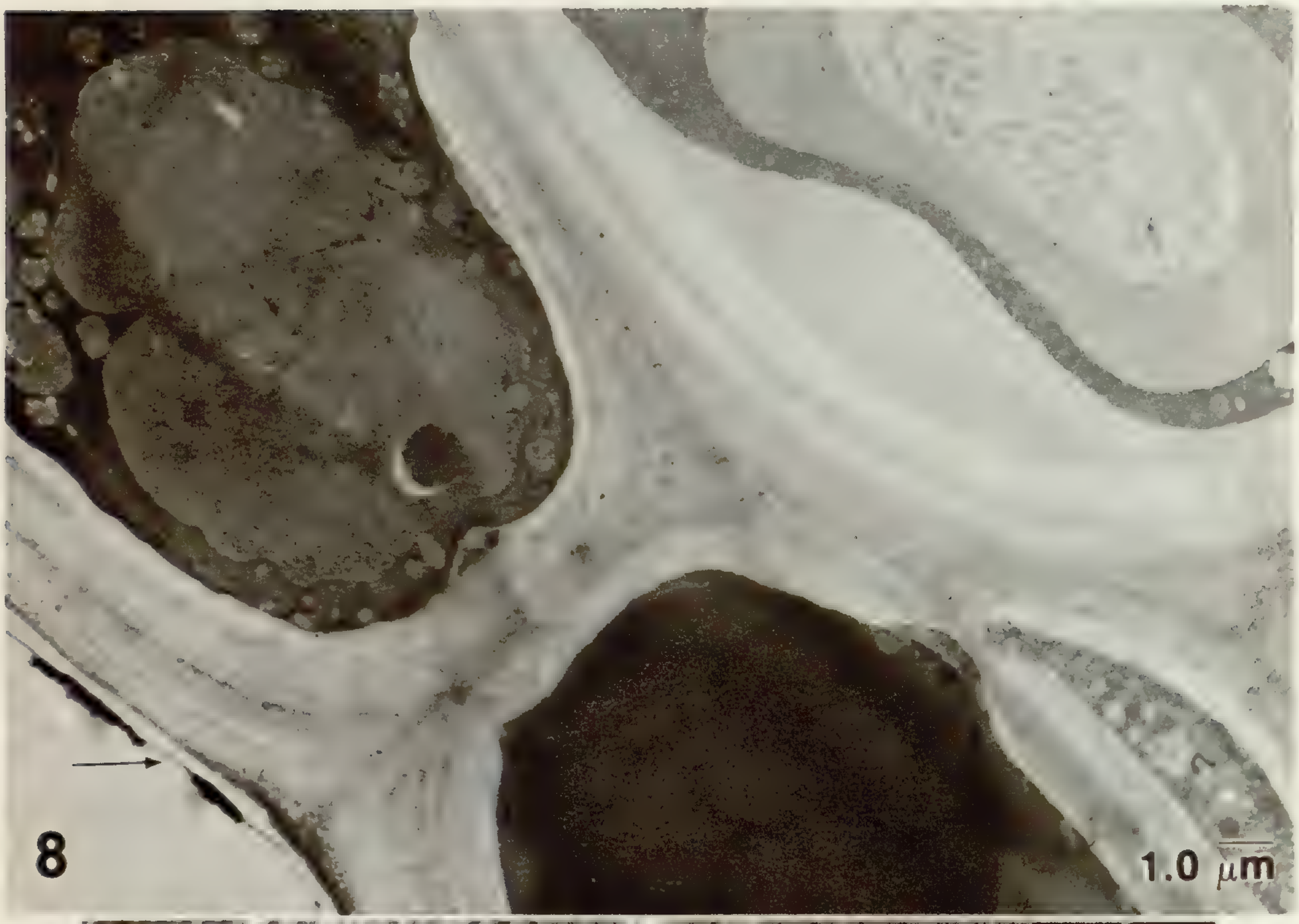
In addition to these three differentiated regions, the adjoining meristele undergoes certain modifications. The part of the meristele next to the basal region enlarges with the formation of two or three layers of cells inside the endodermis (Figs. 1 and 2). These cells are somewhat larger than surrounding pericycle cells, cuboidal, and densely staining with very granular cytoplasm, large nuclei, and no vacuoles. The neighboring pericycle cells are somewhat smaller and variable in size, vacuolated, and form only one cell layer. These modified pericycle parenchyma cells appear quite similar to the basal cells in light microscopy (Fig. 2). The endodermis also undergoes modification in this region. Large vacuoles are evident in both light microscopy (Fig. 2) and TEM. No Casparian strip is evident in this region during the crozier stage (secretory phase) of development. Only after the frond has expanded fully and nectaries have ceased functioning does the Casparian strip begin to form.

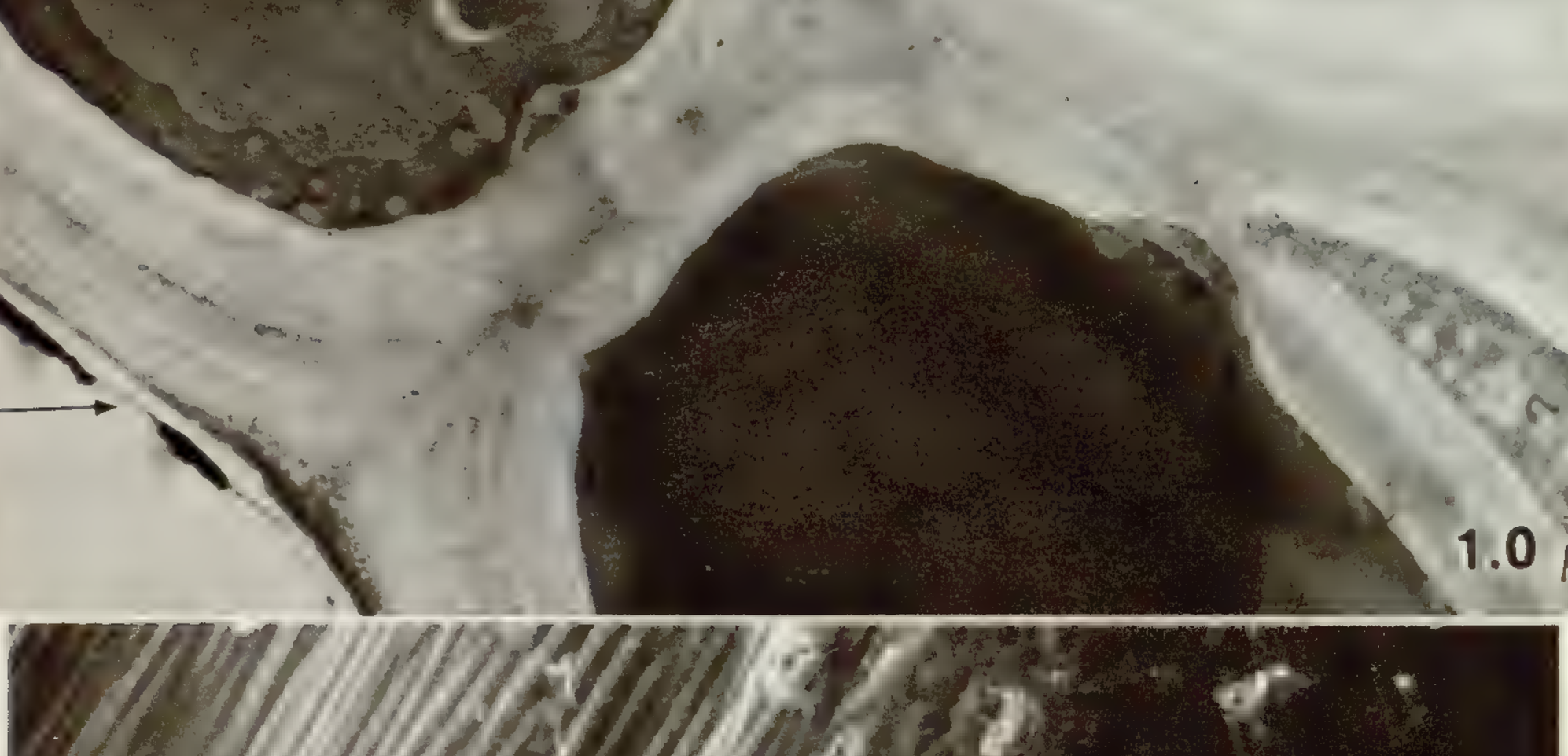
The vascular tissue, composed of sieve cells, xylem tracheids and vessels, and parenchyma cells (Figs. 1 and 2), is modified in content but not in structure. Light microscopy reveals the presence of safranin-stained globules within the sieve cells. Electron microscopy shows a large lumen characteristic of the sieve cell with remnants of cytoplasm near the periphery. A plasmalemma surrounds the lumen and abuts the primary cell wall. Some sieve cells contain an amorphous fibrillar material.

All sieve cells contain refractive spherules, located both centrally and peripherally in the lumen (Figs. 12 and 13). Bounded by single unit membranes, the spherules range in size from 0.1 to 0.7 μm. These spherules tend to aggregate

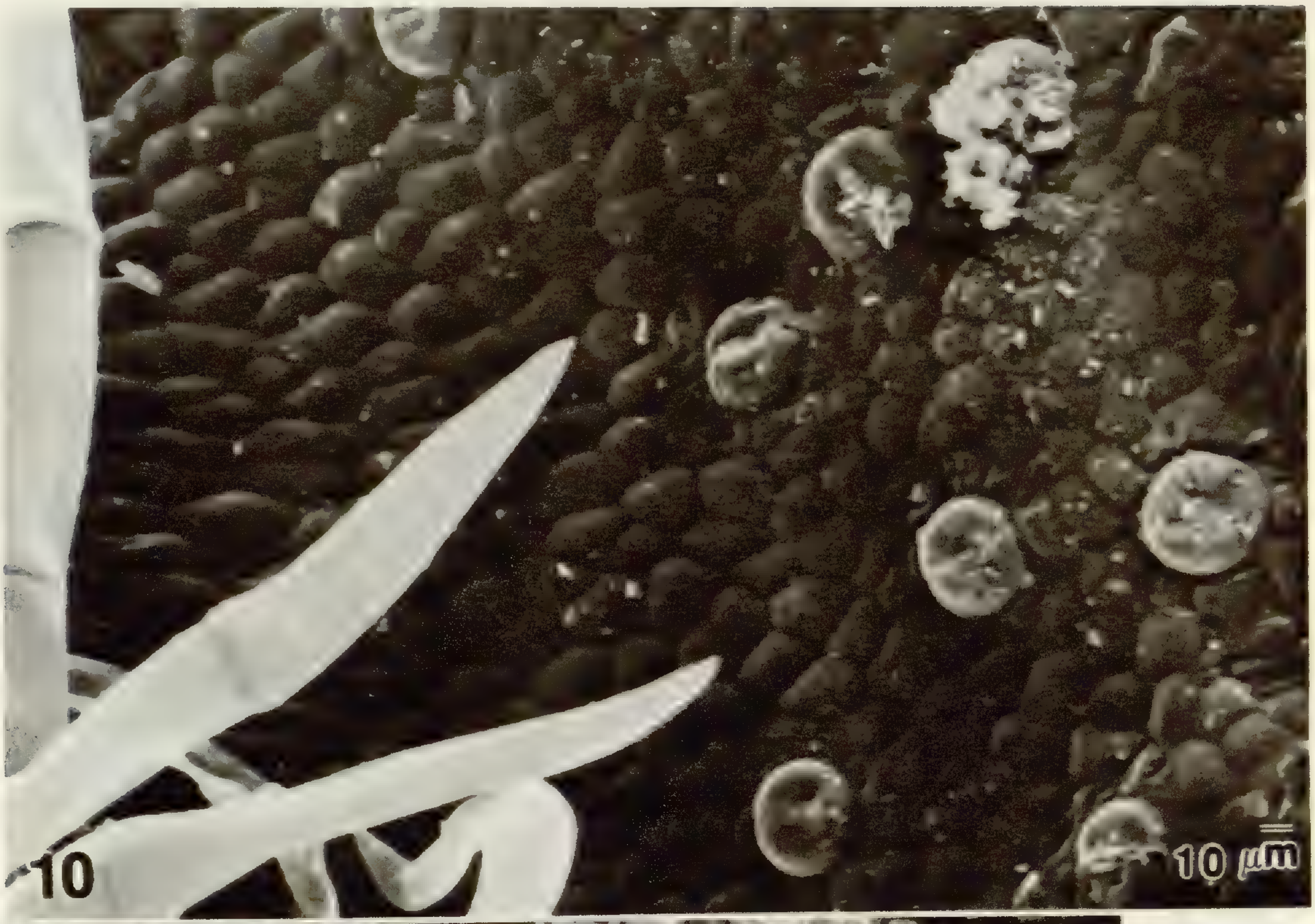


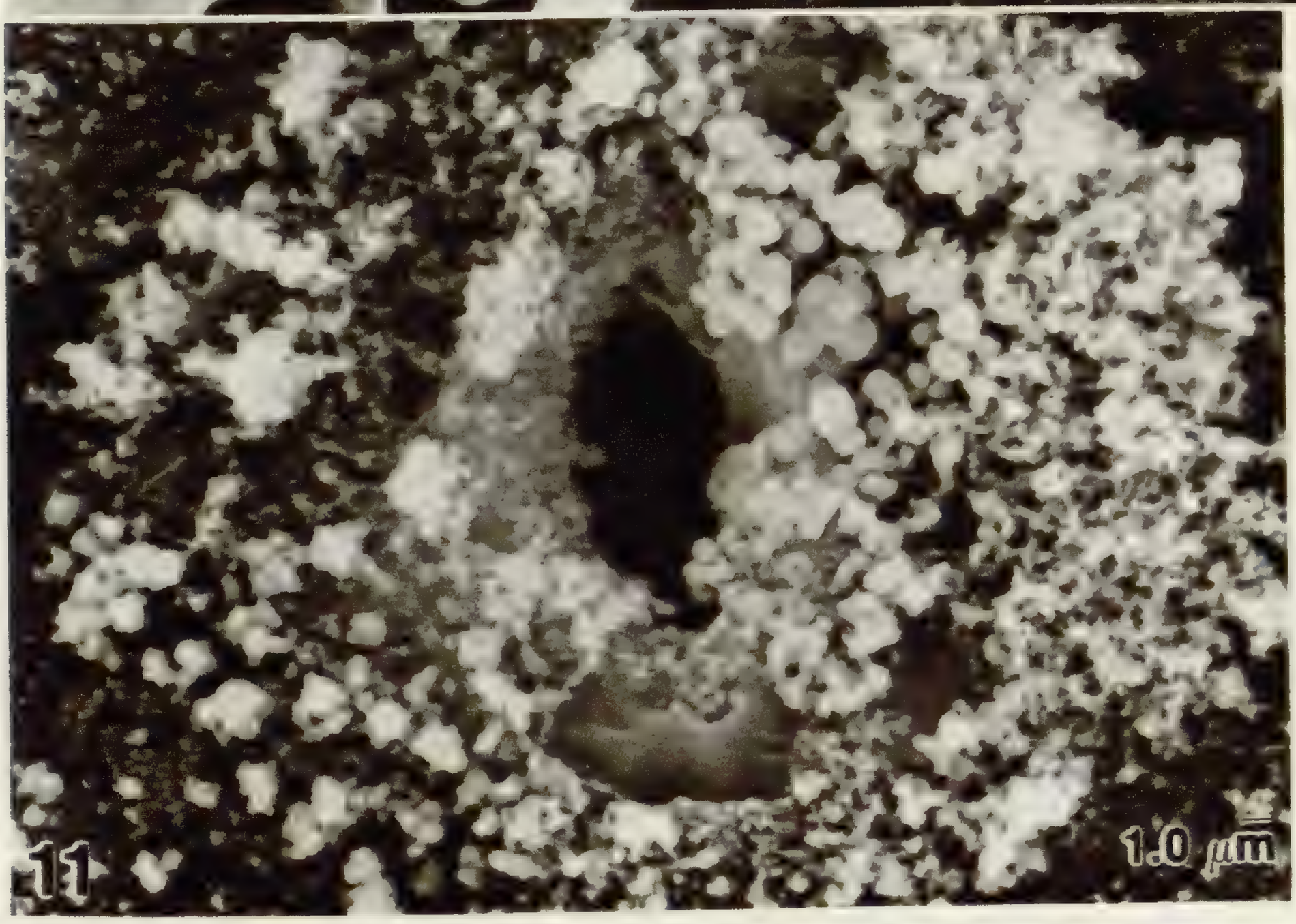
FIGS. 6 and 7. Ultrastructure of secretory nectary cells. FIG. 6. TEM of plasmodesma strand connecting cortical secretory cells. Within the plasmodesma are multivesicular bodies (right arrow) and ER (left arrow). Upper cell shows portion of nucleus (n). FIG. 7. SEM of the epidermal region around stoma. Two or three layers of cells in the epidermal region can be seen. The cuticle layer extends down into the stomate (arrow).





FIGS. 8 and 9. Epidermal layer of nectary. FIG. 8. TEM of the epidermal layer showing thin cuticle (arrow) and vacuoles with electron dense material. FIG. 9. SEM of nectary surface showing isodiametric cells and more numerous stomates as opposed to the elongated cells and very few stomates of the stipe.





FIGS. 10 and 11. Scanning views of nectary epidermis. FIG. 10. SEM of nectary epidermis at cessation of secretion with raised guard cells and trichomes of non-secretory region at left. FIG. 11. Open stomate with globular secretory material.

near the sieve pores which connect the sieve cell to the surrounding parenchyma.

The vascular parenchyma cells stain more densely than the larger sieve cells (Fig. 12). The dense cytoplasm of the parenchyma contains plastids, mitochondria, endoplasmic reticulum, vesicles, and vacuoles. The vesicles and vacuoles contain a fibrillar material similar to that in the sieve cells (Fig. 13). Dictyosomes are not evident in these cells.

Vascular parenchyma and sieve cells are interconnected by plasmodesmata, which join the parenchyma to the sieve pore areas of the sieve cell (Warmbrodt & Evert, 1974a and 1974b). ER may line the interior of these cytoplasmic connections. Figure 12 indicates the location of some of the plasmodesmata.

The developmental stage of the frond determines the structure and functioning of the nectaries of *Pteridium aquilinum*. The nectaries differentiate and function only during the crozier stage. With maturation of the frond, the nectaries cease secreting and some lysigenous degradation is noted in the tissue (Fig. 1). Secondary cell walls are formed in most cells, fewer globules and more tannins are seen in the secretory cells, a Casparian strip forms in the endodermal cells, and the stomata become closed (Fig. 10).

Discussion

Studies of the ultrastructure of nectaries and the possible function of the cells have emphasized angiosperms. It is interesting to compare data derived from angiosperms with these observations of the *Pteridium* nectary. In angiosperm nectaries vascular tissue is generally separated from the secretory cells by nonglandular or subglandular parenchyma (Durkee, 1983). Characteristics of these cells include abundant mitochondria, well-developed vacuoles, large numbers of plasmodesmata, less dense cytoplasm, and less developed ER than the secretory cells. In *Pteridium* the cells of the basal region are well vacuolated, have granular cytoplasm, many mitochondria, and plastids, and are tightly packed in contrast to the surrounding parenchyma cells. Thus they possess most of the characteristics of subglandular parenchyma cells.

Although there is no specialized vascular tissue supplying the nectary in *Pteridium*, the vascular strand of the meristele is only a few cells distant from the secretory cells. Furthermore, the cells of the pericycle and endodermis are highly modified in the region of the nectary. These cells are similar to the basal parenchyma but lack the extensive development of vacuoles. The Casparian strips of the endodermal cells are not developed. Such changes in this region of the meristele may facilitate transport of the pre-nectar (phloem sap) from the phloem to the secretory parenchyma of the nectary. Durkee (1983) reported that a common component of the parenchyma cells in the phloem of *Passiflora* nectaries is membrane-bound fibrillar material (proteinaceous) and that rough ER is abundant. Vesicles containing fibrillar material and abundant ER can be seen in the vascular parenchyma cells of *Pteridium* (Fig. 13).

According to Fahn (1979b), the secretory cells of some angiosperm nectaries are characterized by increased numbers of mitochondria, increased amount of

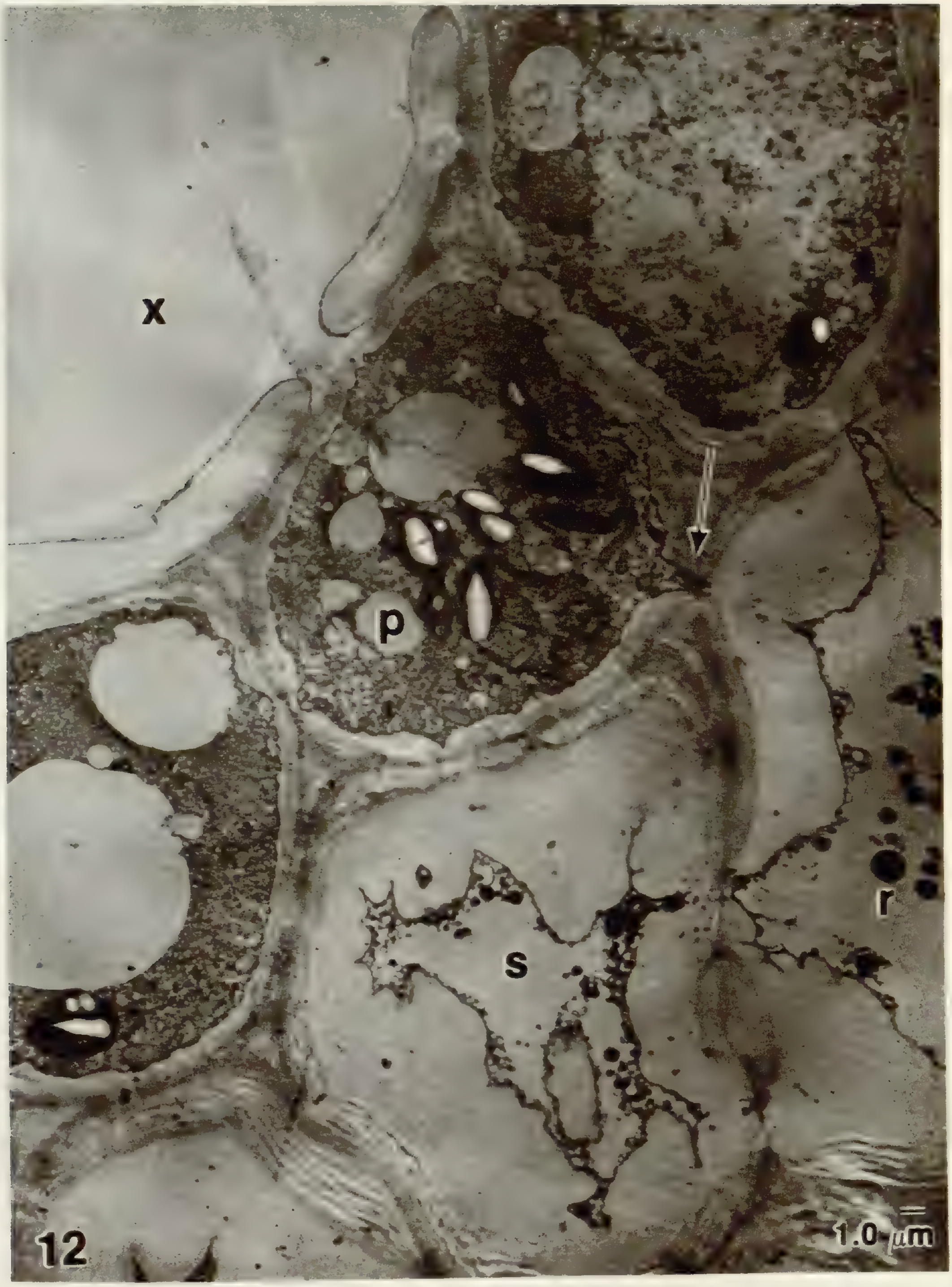


FIG. 12. TEM section of the vascular tissue with xylem element (x), vascular parenchyma (p) and sieve cells (s) containing refractive spherules (r). Plasmodesmata are seen between vascular parenchyma and sieve cells (arrow). Many small vesicles are present bordering the lumen of the sieve cell.

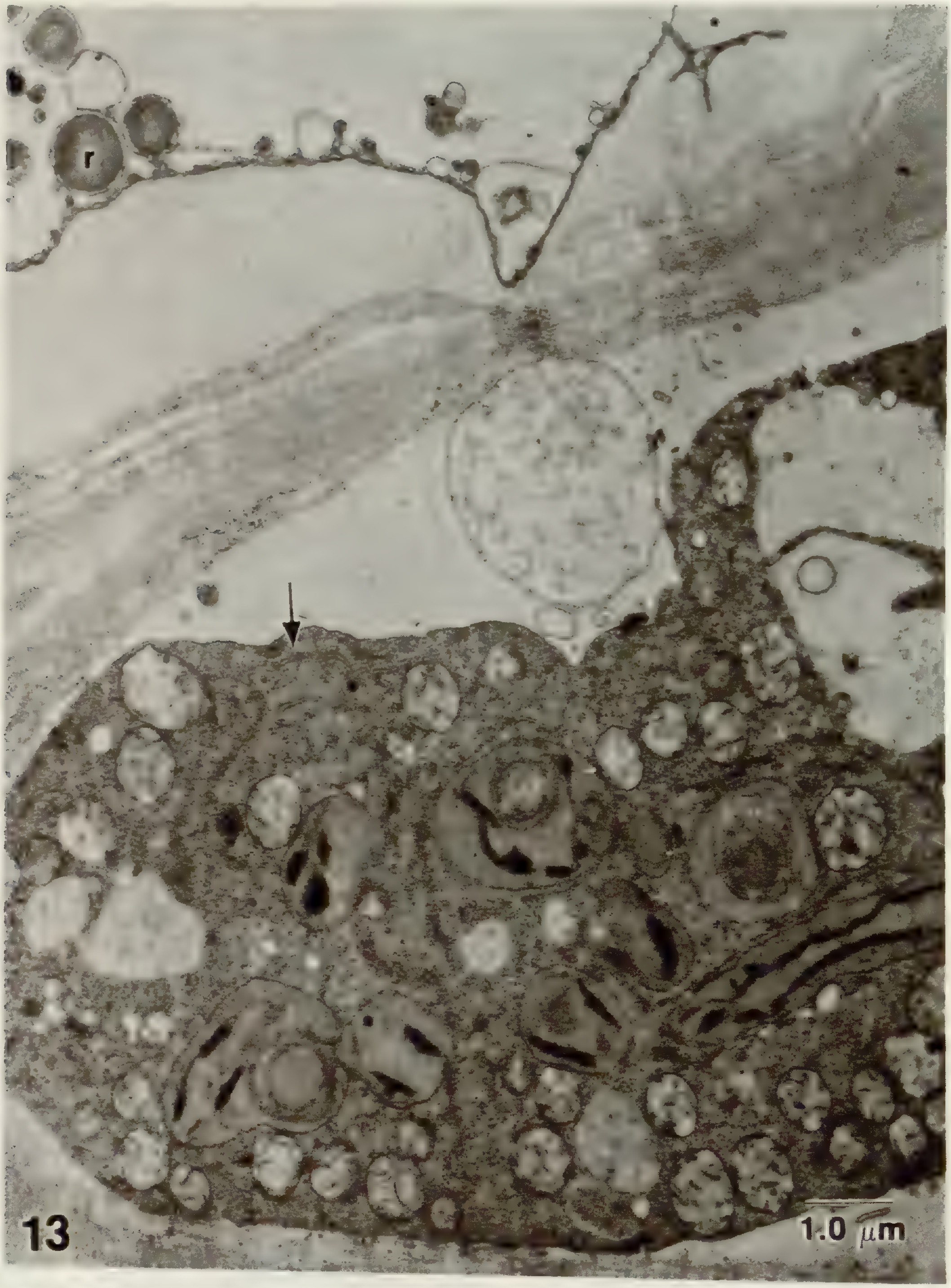


FIG. 13. TEM of sieve cell above and vascular parenchyma cell below, with fibrillar material in vacuoles and in a large membrane-bound organelle between the cytoplasm and the cell wall. Endoplasmic reticulum can be seen in parenchyma cell (arrow). Refractive spherules (r) are obvious in the sieve cell.

ER with swollen cisternae, vesicles, and also, in others, numerous Golgi bodies. These characteristics were all noted in the cortical region of the *Pteridium* nectary. In addition, the distinct differences between the cortical cells of the nectary as opposed to the surrounding cortex of the stipe (Figs. 1 and 2) indicate that they are indeed modified and are probably secretory in function.

The large nucleus which appears to fill most of each cortical secretory cell is almost obscured by the large number and size of safranin-stained red globules. These globules are similar to those seen in sieve cells and vascular parenchyma and represent an increase in size of 2–4 times, possibly indicating modification of the secretion in these cells.

Once the secretion is modified, it may be packaged and/or transported by ultrastructural organelles in the cortical secretory parenchyma before it is released into a substomatal chamber. Ultrastructural organelles involved in this transport of secretory material may include plasmodesmata, endoplasmic reticulum, and multivesicular bodies. Plasmodesmata not only link parenchyma cells to sieve cells in vascular tissue, but they also interconnect the cortical secretory parenchyma cells. They permit symplastic transport to occur throughout nectariferous tissue (Lüttge, 1971).

Durkee (1983) stated that ER is a notable feature in glandular cells, and the ER cisternae sometimes are swollen and vesicles are numerous. In *Pteridium* cortical secretory parenchyma, some ER cisternae are swollen with fibrillar inclusions and many small vesicles are present. A form of packaging and secretion, noted by Fahn and Rachmilevitz (1975), involves vesicles that may bud off from the ends of the cisternae. As vesicles approach the plasmalemma, the membranes may fuse, releasing the fibrillar contents to the outside of the cytoplasm.

Multivesicular bodies are aptly named for their structure because their function remains unclear. Noted in plasmodesmata (Fig. 6), they may function in formation or transport of pre-nectar (Rachmilevitz & Fahn, 1973). Fahn (1979a) noted that multivesicular bodies are often present in active secretory cells and summarized several functions suggested for their role in the secretory process.

Other characteristics of secretory cells also observed in the cortical secretory parenchyma of *Pteridium* include numerous mitochondria, few plastids, reduced vacuoles, and dictyosomes adjacent to the wall.

With the exception of stomates, the epidermal cells covering the surface of the nectary do not appear to be involved directly with nectar secretion. No globules appear within the cells when viewed in light microscopy. Viewed in scanning electron microscopy, however, secretory stomates that are open are covered with a globular material. Closed stomates have none of the material. Since stomates are much more abundant in the epidermis of the nectary than in the rest of the stipe, they appear to be involved with more than respiration and gas exchange. Stomates, described as modified when they are coupled with secretion, usually remain open (Fahn, 1979a). However, closed stomates do occur on nectary surfaces.

The ultrastructure of the nectaries of *Pteridium aquilinum* indicates that most of the organelles and cell types associated with vascularized angiosperm nec-

taries are present in these fern nectaries. The *Pteridium* nectaries are definitely structured nectaries, contrary to Fahn's (1979a) description of them as undifferentiated and Page's (1982) statement that they are composed only of small, isodiametric parenchymatous cells with dense protoplasmic contents.

Field observations by Page (1982) indicate a secretory period from six days to about four weeks. There are corresponding anatomical changes that occur in the nonfunctional nectary following cessation of secretion. These changes in cell structure appear to occur from the epidermal region centripetally (Fig. 1). Epidermal cell walls become thickened first and the stomata are occluded (Fig. 10). In the cortical secretory parenchyma the globules decrease and tannins become more obvious. These cells also begin to form secondary cell walls. Lignification occurs in most cells and the endodermis forms a Casparian strip in the cells within the nectary region.

The anatomy of *Pteridium* nectaries correlates with field observations and with the reported examples of other structured nectaries. Durkee (1983) noted that research studies of nectaries should be concerned with ultrastructural detail, the nature and function of subglandular tissue, and the vascular supply to nectaries in regard to phloem physiology. The presence of modified tissue in the nectary and simple sieve cells in the phloem would appear to make *Pteridium* an excellent tool for physiological studies of phloem and nectary activity.

Acknowledgments

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Literature Cited

Darwin, F. 1877. On the glandular bodies on *Acacia sphaerocephala* and *Cecropia peltata* serving as food for ants, with an appendix on the nectar-glands of the common brake fern, *Pteris aquilina*. J. Linn. Soc., Bot. 15:398–409.

Durkee, L. T. 1983. The ultrastructure of floral and extrafloral nectaries. Pp. 1–29 in *The biology of nectaries*, eds. B. Bentley and T. Elias. New York: Columbia University Press.

Fahn, A. 1979a. *Secretory tissues in plants*. New York: Academic Press.

———. 1979b. Ultrastructure of nectaries in relation to nectar secretion. Amer. J. Bot. 66:977–985.

——— and T. Rachmilevitz. 1975. An autoradiographical study of nectar secretion in *Lonicera japonica* Thunb. Ann. Bot. (London) 39:975–976.

Lloyd, F. E. 1901. The extra-nuptial nectaries in the common brake, *Pteridium aquilinum*. Science, n.s. 13:885–890.

Lüttge, U. 1961. Über die Zusammensetzung des Nektars und den Mechanismus seiner Sekretion. I. Planta 56:189–212.

———. 1971. Structure and function of plant glands. Annual Rev. Pl. Physiol. 22:23–44.

Mokotoff, G. F. 1978. *Electron microscopy laboratory techniques*. Monroe, New York: Library Research Associates.

Page, C. N. 1982. Field observations on the nectaries of bracken, *Pteridium aquilinum*, in Britain. Brit. Fern Gaz. 12:233–240.

RACHMILEVITZ, T. and A. FAHN. 1973. Ultrastructure of nectaries of *Vinca rosea* L., *Vinca major* L. and *Citrus sinensis* Osbeck cv. Valencia and its relation to the mechanism of nectar secretion. Ann. Bot. (London) 37:1–9.

SCHREMMER, F. 1969. Extranuptiale Nektarien. Beobachtungen an *Salix eleagnos* Scop. und *Pteridium aquilinum* (L.) Kuhn. Oesterr. Bot. Z. 117:205–222.

SPURR, A. R. 1969. A low viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastruct. Res. 26:31–43.

WARMBRODT, R. D. and R. F. EVERT. 1974a. Structure and development of the sieve element in the stem of *Lycopodium lucidulum*. Amer. J. Bot. 61:267–277.

———. 1974b. Structure of the vascular parenchyma in the stem of *Lycopodium lucidulum*. Amer. J. Bot. 61:437–443.

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Notes on ×*Pleopodium* and *Pleopeltis* in Tropical America

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Interpretation of the polypodioid ferns has been a classic problem for pteridologists. The groupings are, with some exceptions, fairly clear, but whether they should be treated as subgenera of *Polypodium* or as distinct genera is a matter of considerable disagreement. There seems to be growing acceptance of their recognition as distinct genera (Smith 1981, 1985; Tryon & Tryon, 1982; Lellinger, 1985; Mickel & Beitel, in press), although some authors continue to recognize *Polypodium* in a broad sense (Proctor, 1977, 1985; Stolze, 1981).

Some of the splinter genera in America (e.g., *Campyloneurum*, *Niphidium*) stand well apart from *Polypodium* s.s., but others are apparently very closely allied to *Polypodium*. This is especially so in regard to *Pleopeltis*, some members of which hybridize with species of *Polypodium* s.s. The best known example of this is *Polypodium* ×*leucosporum* (=*Polypodium lanceolatum* × *P. thyssanolepis*), which was pointed out by Vareschi (1969) and described in detail by Wagner and Wagner (1975), who treated it and its parents within *Polypodium*. Recently, Anthony and Schelpe (1985) described a similar case in southern Africa, in which *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf. (=*Polypodium lanceolatum*) crosses with *Polypodium polypodioides* var. *ecklonii* (Kunze) Schelpe. The authors gave a hybrid intergeneric name to their hybrid species, ×*Pleopodium simianum* Anthony & Schelpe.

In our studies on the ferns of Oaxaca, Mexico (in press), we have seen specimens from various parts of Mexico that involve several members of these two genera. Most of the hybrids have binomials under *Polypodium*. The purpose of this paper is to make several new combinations under ×*Pleopodium* and *Pleopeltis*, and to clarify the putative parentage of the hybrids.

1. ×**Pleopodium leucosporum** (Klotzsch) Mickel & Beitel, comb. nov.—*Polypodium leucosporum* Klotzsch, Linnaea 20:404. 1847.—*Pleopeltis leucospora* (Klotzsch) Moore, Index Fil. 77. 1857.—*Lepicystis leucospora* (Klotzsch) Diels, in Engler & Prantl, Natur. Pflanz. 1(4):324. 1899.—TYPE: Venezuela ["Colombia"], *Moritz 306* (B!; isotype NY!).

Hybrid between *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf. (*Polypodium lanceolatum* L.) and *Polypodium thyssanolepis* A. Br.

Distribution.—Costa Rica, Colombia, Venezuela, Hispaniola.

Discussion.—Wagner and Wagner (1975) studied this hybrid in considerable detail. This combination is especially complicated since both parents have diploid and tetraploid races (Evans, 1963; Wagner & Wagner, 1975; Walker, 1966, 1973), resulting in theory in at least four types of crosses: diploid *Pl. macrocarpa* with two cytotypes of *P. thyssanolepis* and tetraploid *Pl. macrocarpa* with two

TABLE 1. Comparison of ×*Pleopodium leucosporum* and its Parents.

	macrocarpa	*leucosporum*	*thyssanolepis*
Blade	simple	irregularly lobed	pinnatifid
Rhizome scales	erose	fimbriate	fimbriate
Veins	pleopeltid	intermediate	goniophlebioid
Blade scales	round, 0.3–0.4 mm diam.	intermediate	lanceolate, 0.6–1.5 mm long, with elongate tip
	over 1 mm apart	intermediate	close to overlapping
Soral scales	black-centered	lacking	lacking
Spores	normal	abortive	normal

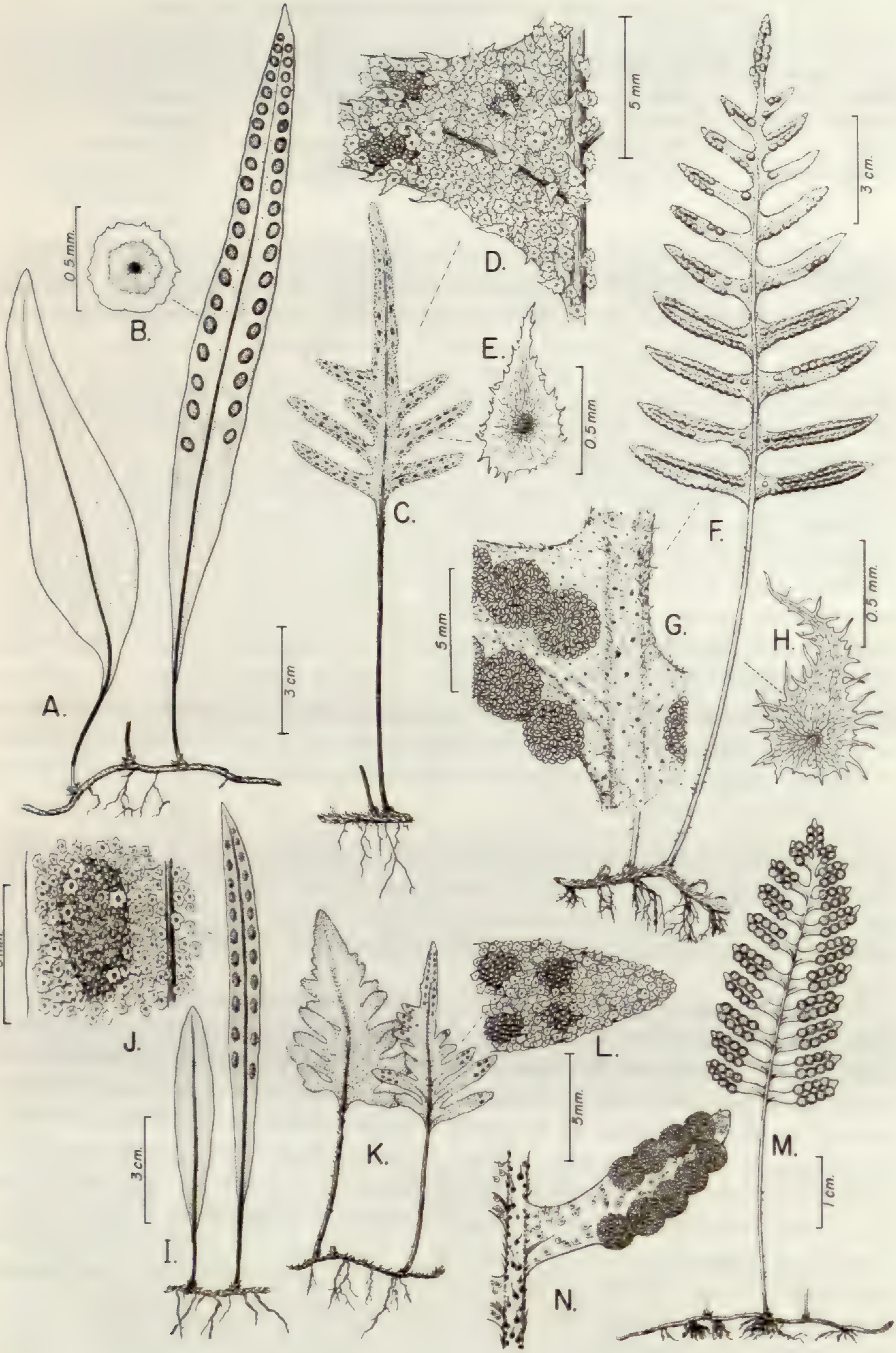
cytotypes of *P. thyssanolepis*. All of these hybrids have abortive spores but differ in the contributions of the two parents, explaining the considerable variation of this hybrid (Wagner & Wagner, 1975; Table 1).

Polypodium thyssanolepis is quite common in Mexico, but there does not seem to be any true *Pleopeltis macrocarpa* in Mexico, at least in Oaxaca and north. (*Pleopeltis macrocarpa* is distinguished by a combination of characters: black-centered soral scales, scattered fimbriate laminar scales, and black-centered, non-comose rhizome scales with conspicuous lumina.) Rather, Weatherby's (1922) varieties (our species) take its place and most of them are involved in crosses with species of *Polypodium*.

2. ×**Pleopodium tricholepis** Mickel & Beitel, hybr. nov. (Fig. 1C–E).—TYPE: Mexico, Oaxaca, Distrito Etla-Cuicatlán, 39 km N of Rte 190 past Telixtlahuaca, mixed oak-juniper forest along stream banks, 6200′, 8 Oct 1969, *Mickel 3873* (NY!; isotype UC!).

Planta inter *Pleopeltim mexicanam* et *Polypodium thyssanolepidem* hybrida a parentibus frondium divisione intermedia et sporis abortivis differt. [Gr., *thrix*, hair, and *lepis*, scale, referring to the ciliate (comose) scales and also a combination of the parental species epithets (*Polypodium trichophora* = *Pleopeltis mexicana*)].

Rhizome creeping, 1.5–2 mm diam.; rhizome scales deeply fimbriate, dimorphic; rhizome scales 1.5–2 mm long, bicolorous with brown-black center and narrow pale brown margin, occasionally with long brown hairs from central point; scales at base of stipe 2–3 mm long, pale brown with or without short dark central streak; fronds distant to nearly clumped; stipe ca. ½ of frond length, castaneous to atropurpureous, densely clothed with bicolorous scales, reddish brown with pale brown laciniate margin, round (0.5–0.8 mm wide) to lanceolate (1.5–2 mm long); blade irregularly pinnatisect, 16–18 cm long, 5–6 cm wide, broadest at base; pinnae or lobes 4–6 pairs, 5–7 mm wide; abaxial surface with scattered to dense, deeply fimbriate scales, mostly lanceolate (1.0–1.5 mm long), some round (0.8–1.0 mm wide), with brown center grading to whitish margin; midrib dark with lanceolate scales, 1.5–2 mm long; adaxial surface with sparse, deeply lacerate, lanceolate scales; sori round to slightly ovate, surrounded by


A.
0.5 mm.
B.
3 cm.
C.
5 mm
D.
0.5 mm
E.
3 cm.
F.
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G.
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H.
5 mm.
J.
3 cm.
I.
5mm.
K.
1 cm.
L.
M.
N.

TABLE 2. Comparison of ×*Pleopodium tricholepis* and its Parents.

	mexicana	*tricholepis*	*thyssanolepis*
Blade	simple	irregularly lobed	pinnatifid
Rhizome scales	dimorphic	dimorphic	monomorphic
	densely comose	occasionally comose	non-comose
	margin denticulate	fimbriate	fimbriate
	0.8–1 mm long (1.5–2 mm at stipe base)	1.5–2 mm long (2–3 mm at stipe base)	3–4 mm long
Stipe	flattened	slightly flattened	terete
Abaxial laminar scales	sparse	scattered to dense	dense
	round, 0.3–0.5 mm diam.	some round, mostly lanceolate, 1–1.5 mm long	lanceolate, 0.6–1.5 mm long
Hydathodes	lacking	present	present
Soral scales	present, round, erose	rare, lanceolate, fimbriate	lacking
Spores	normal	abortive	normal

laminar scales; soral scales rare, peltate to cordate, lanceolate, 0.8 mm long with pale brown point of attachment and lighter brown fimbriate margin; spores abortive.

Distribution.—Epiphytic in oak-juniper woods. Known only from the type collection.

Discussion.—This specimen, exhibiting hybrid characters of abortive spores and irregular blade lobes, appears to represent a hybrid between the pinnatisect species *Polypodium thyssanolepis* (Fig. 1F–H) and a simple-bladed species of *Pleopeltis* (see Table 2). Although *P. conzattii* was the only species of *Pleopeltis* found at the same locality, the presence of round scales and the absence of black-centered rachis scales makes that species unlikely as a possible parent. The few soral scales are not strongly and deeply bicolorous as one would expect in hybrids involving *P. polylepis*, *P. crassinervata*, *P. astrolepis*, and *P. interjecta*. *Pleopeltis mexicana* (Fig. 1A, B), with lightly colored soral scales, long stipe, and occasional tufts of long hairs on the rhizome scales, is probably the other parent.

Another specimen (Mexico, DF, Angostura, 2600 m, *Lyonnet 3414*, US) has rhizome scales monomorphic and larger (2–2.5 mm long vs. 1.5–2), blade scales darker, farther apart (sparse), and smaller (0.8–1 mm long vs. 1–1.5), pinna pairs

←

FIG. 1. Hybrids of ×*Pleopodium* and their putative parents. A, B. *Pleopeltis mexicana* (*Mickel 4357*, NY, Oaxaca). A. Habit. B. Abaxial blade scale. C–E. ×*Pleopodium tricholepis* (*Mickel 3873*, NY, holotype). C. Habit. D. Abaxial blade detail. E. Abaxial blade scale. F–H. *Polypodium thyssanolepis* (*Mickel 7065*, NY, Oaxaca). F. Habit. G. Abaxial blade detail. H. Abaxial blade scale. I, J. *Pleopeltis polylepis* (*Mickel 7065*, NY, Oaxaca). I. Habit. J. Abaxial blade detail. K, L. ×*Pleopodium bartlettii* (*Bartlett 10286*, US, holotype). K. Habit. L. Abaxial blade detail. M, N. *Polypodium polypodioides* var. *aciculare* (*Mickel 1019*, NY, Oaxaca). M. Habit. N. Abaxial blade detail.

TABLE 3. Comparison of ×*Pleopodium bartlettii* and its Parents.

	polylepis	*bartlettii*	*polypodioides*
Blade	simple	irregularly lobed	pinnatifid
Rhizome scales	rarely comose	non-comose	non-comose
Laminar scales:			
Abaxial	round dark red-center 0.5–1 mm diam.	round & lanceolate red-brown center 0.1–0.3 mm diam.	round & lanceolate dark brown center 0.1–0.3 mm diam. or 0.4–0.6 mm long
Adaxial	round, erose	round base with long tip, some round	minute base with long tip
Soral scales	round	round	lacking
Spores	37–45 μm (42.2)	37–42 μm (38.5)	37–42 μm (39.7)

fewer, and soral scales dark-centered (vs. pale brown-centered). Tentatively we consider it as a variant of ×*P. tricholepis*, but conceivably it may represent the hybrid of *Pleopeltis interjecta* × *Polypodium thyssanolepis*.

3. ×**Pleopodium bartlettii** (Weath.) Mickel & Beitel, comb. et stat. nov. (Fig. 1K, L).—*Polypodium bartlettii* Weath. (pro sp.), Amer. Fern J. 25:56. 1935.—TYPE: Mexico, Tamaulipas, vicinity of San José, on tree trunks, *Bartlett 10286* (US!; isotype fragment GH!).

Hybrid between *Pleopeltis polylepis* (Roemer ex Kunze) Moore (Fig. 1I, J) and *Polypodium polypodioides* (L.) Watt (Fig. 1M, N) (Table 3), as suggested by Weatherby (1935), who noted similarities with *P. leucosporum*; he also thought it might be an odd form of *P. lanceolatum*. Reproductive status unknown.

Distribution.—Known only from the type collection.

4. ×**Pleopodium fallacissimum** (Maxon) Mickel & Beitel, comb. et stat. nov. (Fig. 2F, G).—*Polypodium fallacissimum* Maxon (pro sp.), Contr. U.S. Natl. Herb. 17:567. 1916.—TYPE: Mexico, Coahuila, San Lorenzo Canyon, 6 mi SE of Saltillo, *Palmer 426* (US!; isotype NY!).

Hybrid between *Pleopeltis erythrolepis* (Weath.) Pic. Ser. (Fig. 2B–E) and *Polypodium guttatum* Maxon (Fig. 2H–J) (see Table 4), as suggested by Thomas Wendt [note on paratype at US and pers. comm. as *polylepis* ×*guttatum*; he considered *erythrolepis* as a variety of *polylepis* (Wendt, 1980)]. Reproductive status unknown.

Distribution.—Southern Coahuila.

Discussion.—The paratype, *Palmer 425*, is smaller and less lobed, and is probably just a smaller form of *Pleopeltis fallacissimum*. *Heteroneuron paradoxum* Fée was cited by Fournier as a synonym of *Polypodium thyssanolepis*, but Maxon suggested it might be *Polypodium fallacissimum*. It is difficult to determine with certainty from Fée's illustration (Mém. foug. 6:3, pl. 1, f. 4. 1854). On general form it looks as if it might be a dwarf form of *P. thyssanolepis*, but in the

description Fée says there are scales among the sporangia, suggesting that *Pleopeltis* is involved.

In our work on Oaxacan pteridophytes (in press), we are treating the traditional varieties of *Polypodium lanceolatum* (*Pleopeltis macrocarpa*) as distinct species, necessitating two new combinations under *Pleopeltis*.

Pleopeltis interjecta (Weath.) Mickel & Beitel, comb. nov.—*Polypodium peltatum* Cav. var. *interjectum* Weath., Amer. Fern J. 34:17. 1944.—*Pleopeltis macrocarpa* var. *interjecta* (Weath.) A. R. Smith, Amer. Fern J. 70:26. 1980.—TYPE: Guatemala, Chimaltenango, 2700 m, *Standley 60957* (F).

Pleopeltis mexicana (Fée) Mickel & Beitel, comb. nov. (Fig. 1A, B).—*Drynaria mexicana* Fée, Mém. foug. 8:97. 1857.—SYNTYPES: Mexico. Veracruz, *Galeotti 6321*; Puebla, *Schaffner 179*; Popocatepetl, *Schaffner 292* (P?).

Polypodium lanceolatum L. var. *trichophorum* Weath., Contr. Gray Herb. 65: 8. 1922.—TYPE: Mexico, lava fields near Eslaba, 8000′, *Pringle 11797* (GH!; isotype US!).

The type of *Pleopeltis* (*Pl. angusta*) is pinnate, but as commonly construed the genus is comprised mostly of species with undivided fronds. The genus is distinguished by its peltate scales in the sorus. *Polypodium* (*Pleopeltis*) *percussum* Cav. seems to lack them, even in the very young sori, and might better be considered a *Microgramma*. Conversely, some species often treated as *Pleopeltis* have peltate soral scales, but in other respects seem disparate, e.g., *Pleopeltis munchii* (Christ) A. R. Smith.

One species usually treated as a *Polypodium*, *P. fallax*, has peltate soral scales, and therefore we are placing it in *Pleopeltis*. Another interesting feature of this species is its comose rhizome scales, which are present in nearly all species of *Pleopeltis* in Mexico. Such scales are also common in *Pecluma* and only occasionally in *Polypodium*, e.g., *P. adelphum* Maxon.

Pleopeltis fallax (Schlecht. & Cham.) Mickel & Beitel, comb. nov. (Fig. 2S–U).—*Polypodium fallax* Schlecht. & Cham., Linnaea 5:609. 1830.—TYPE: Mexico, [Veracruz], Misantla, *Schiede & Deppe 758* (B!, photo BM!; isotype LE!).

Pleopeltis fallax apparently hybridizes with two other species of *Pleopeltis*. (If *Pl. fallax* is maintained in *Polypodium*, then these hybrids would fall into ×*Pleopodium*.)

Pleopeltis ×sordidula (Maxon & Weath. in Weath.) Mickel & Beitel, comb. et stat. nov. (Fig. 2P–R).—*Polypodium sordidulum* Maxon & Weath. in Weath. (pro sp.), Amer. Fern J. 17:92. 1927.—TYPE: Mexico, Veracruz, epiphytic in coffee trees near Cordoba, *Spence 114* (GH!; isotype US!).

Since the original description of this species included both this and the following hybrid, we are redescribing *Pl.* ×*sordidula* [hybrid between *Pleopeltis astrolepis* (Liebm.) Fourn. (Fig. 2L–O) and *Pl. fallax* (Fig. 2S–U)] here in a more restricted sense.

Rhizome creeping, 0.5–0.8 mm diam.; rhizome scales 0.1–0.3 mm diam., round,

A.
3 cm.
B.
C.
5 mm
D.
0.5 mm.
E.
2 cm
F.
G.
H.
3 cm
0.5 mm.
I.
J.
5 mm.
K.
2 cm.
L.
3 cm.
0.5 mm.
M.
N.
5 mm.
O.
0.5 mm
P.
Q.
R.
S.
2 cm.
T.
U.

TABLE 4. Comparison of ×*Pleopodium fallacissimum* and its Parents.

	erythrolepis	*fallacissimum*	*guttatum*
Blade	simple	irregularly lobed	pinnatifid
Rhizome scales	margin cells lengthwise	margin cells toward margin	margin cells toward margin
	sclerotic	sclerotic-clathrate	sclerotic-clathrate
	comose	non-comose	non-comose
Stipe	flattened	flattened	terete
Laminar scales:			
Abaxial	dense	sparse to scattered	sparse
	round & lanceolate	deltate-ovate	deltate-ovate
	non-clathrate	subclathrate	clathrate
	emarginate	marginate	marginate
	brown center	dark only at attachment	no dark center
Adaxial	linear-lanceolate	lanceolate	lacking
	fimbriate	denticulate	
	dark center	no dark center	
Hydathodes	lacking	present	present
"Stretch marks" (epidermal lines)	present	present	lacking
Soral scales	frequent	rare	lacking
	dark brown center	clathrate center	
	brown to light brown margin	light brown margin	

bicolorous, with dark brown to black center with narrow whitish margin, comose from central point with 0.5–0.7 mm reddish brown hairs, margin entire; fronds distant, stipe ¼–⅙ of frond length, flattened, atropurpureous, scales bicolorous, round with comose center; blade irregularly pinnatifid, 4–7 cm long, 0.5–1.0 cm wide, linear-lanceolate, with acuminate tip; abaxial lamina with sparse fimbriate scales, some lanceolate (0.5–0.7 mm long), some round (0.1–0.3 mm diam.), with semi-clathrate center and tan to whitish tan margin; midrib dark with scattered lanceolate scales with dark sclerotic center; lateral veins obscure; adaxial lamina with sparse scales similar to abaxial scales except more deeply cut; soral scales

←

FIG. 2. Hybrids of ×*Pleopodium* and *Pleopeltis* and their putative parents. A. *Pleopeltis crassinervata* (*Hallberg 1389*, NY, Oaxaca), habit. B–E. *Pleopeltis erythrolepis* (*Correll & Gentry 22975A*, NY, Chihuahua). B. Habit. C. Abaxial blade detail. D. Abaxial blade scale. E. Adaxial blade scale. F, G. ×*Pleopodium fallacissimum* (*Palmer 426*, NY, isotype). F. Habit. G. Abaxial blade scale. H–J. *Polypodium guttatum* (*Rzedowski 24040*, NY, Edo. Mexico). H. Habit. I. Abaxial blade detail. J. Abaxial blade scale. K. *Pleopeltis melanoneuron* (*Purpus 5798*, US, holotype), habit. L–O. *Pleopeltis astrolepis* (*Mickel 5165*, NY, Oaxaca). L. Habit. M. Abaxial blade scale. N. Abaxial blade detail. O. Rhizome scale. P–R. *Pleopeltis* ×*sordidula* (*Copeland 149*, US). P. Habit. Q. Stipe detail. R. Rhizome scale. S–U. *Pleopeltis fallax* (*Mickel 6468*, NY, Oaxaca). S. Habit. T. Abaxial blade detail. U. Abaxial blade scale.

TABLE 5. Comparison of *Pleopeltis* ×*sordidula* and its Parents.

	astrolepis	*sordidula*	*fallax*
Blade	simple	irregularly lobed	pinnate-pinnatifid to pinnate-bipinnatifid
Rhizome scales	bicolorous black center/pale brown margin	bicolorous black center/whitish margin	concolorous black
	ovate, 0.3–0.5 mm long	round, 0.1–0.3 mm diam.	round, 0.3–0.5 mm diam.
	comose	comose	comose
Stipe	short, flattened	short, slightly flattened	long, terete
Rachis scales	black sclerotic	brown with sclerotic center	clathrate
Laminar scales:			
Abaxial	scattered	sparse	sparse
	lanceolate (0.5–1 mm) to round (0.3–0.5 mm)	lanceolate (0.5–0.7 mm) to round (0.1–0.3 mm)	lanceolate (0.5–0.8 mm)
	bicolorous	bicolorous	concolorous
	dark brown center/pale brown margin	brown center/pale brown to whitish margin	brown
	non-clathrate	semiclathrate	clathrate
Adaxial	as abaxial	as abaxial	lacking
Sori	elongate	elongate	round
Spore size	44–51 μm (47.1)	38–45 μm (41.8)	37–45 μm (40.1)

extremely rare, round to lanceolate (0.3–0.5 mm long), dark brown to brown center, with light brown fimbriate margin; sori slightly oval; spores appearing normal.

Additional collections: Mexico. Veracruz: Río Blanco, 4800′, *Fisher 37* (US); Metlac [near Fortín de las Flores], 900 m, *Copeland 149* (US).

Polypodium sordidulum was based on three specimens from Veracruz. Maxon and Weatherby considered it "a local offshoot of *P. astrolepis*." They believed it to be similar to *P. astrolepis* except for the lobing, subterete stipe, and orbicular sori (although the figure shows them as oblong).

The type specimen and one of the two paratypes (*Fisher 37*) appear to represent the hybrid combination of *Pleopeltis astrolepis* × *Pl. fallax*; the other paratype (*Purpus 5798*) differs in several characters from this taxon. These differences, which may be due to its presumed origin as the hybrid of *Pleopeltis fallax* and *Pl. crassinervata*, will be discussed under the next hybrid.

Pleopeltis ×*sordidula* (see Table 5) has the irregularly lobed blade of a hybrid between a simple-bladed parent (*Pl. astrolepis*) and a more divided parent (*Pl. fallax*), with blade scale distribution (on both abaxial and adaxial surfaces, although the scales are sparse rather than scattered), and type (round and lanceolate rather than just lanceolate as in *Pl. fallax*) as in *Pl. astrolepis*, whereas coloration of the scales has characters of both parents (bicolorous as in *Pl. as-*

TABLE 6. Comparison of *Pleopeltis* ×*melanoneuron* and its Parents.

	crassinervata	*melanoneuron*	*fallax*
Blade	simple	irregularly lobed	pinnate-pinnatifid to pinnate-bipinnatifid
Rhizome scales	lanceolate 1–1.5 mm long bicolorous dark brown center/wide pale brown margin comose	lanceolate 0.5–0.8 mm long bicolorous dark brown to black center/narrow pale brown margin comose	round 0.3–0.5 mm diam. concolorous black comose
Rachis scales	non-comose lanceolate	non-comose lanceolate	comose round
Laminar scales:			
Abaxial	scattered lanceolate (0.8 mm long) and round (0.5 mm diam.) bicolorous brown center/pale brown margin	sparse lanceolate (0.5 mm long) and round (0.5 mm diam.) bicolorous brown center/pale brown margin	sparse lanceolate (0.3) 0.5–0.8 mm long concolorous clathrate
Adaxial	as abaxial	as abaxial	lacking
Lateral veins	dark, evident	dark, evident	obscure

trolepis, semiclathrate center as in the clathrate scales of *Pl. fallax*). The short, slightly flattened stipes are intermediate between the short, strongly flattened stipe of *Pl. astrolepis* and the terete stipe of *Pl. fallax*; the bicolorous rachis scales are also intermediate between its two parents.

Pleopeltis ×melanoneuron Mickel & Beitel, hybr. nov. (Fig. 2K).—TYPE: Mexico, Veracruz, Zacuapan, Jan 1912, *Purpus 5798* (US!; isotype UC).

Planta inter *Pleopeltim crassinervatam* et *P. fallacem* hybrida a parentibus frondium divisione rhizomatisque squamis intermedia differt et a *P.* ×*sordidula* nervis nigris laminaeque apice acuta abstat. (Gr., *melos*, black, and *neuron*, vein, referring to the dark secondary veins at the base of the blade.)

Rhizome creeping, 0.5–0.8 mm diam.; rhizome scales 0.5–0.8 mm long, lanceolate, with dark brown to black center and narrow pale brown margin, comose from central point with 0.5–0.8 mm reddish brown hairs, margin fimbriate; fronds distant; stipe ca. ¼ of frond length, round, atropurpureous; blade irregularly pinnatifid, 4.3–5.5 cm long, 1.0–1.8 cm wide, oblanceolate, with acute tip, lateral lobes with irregular teeth at tips; abaxial and adaxial surface with sparse fimbriate scales, some lanceolate (0.5 mm long), some round (0.1–0.3 mm diam.), with brown center and pale brown margin; midrib dark with scattered lanceolate scales, 0.8–1.0 mm long, similar in color to laminar scales, lateral veins evident, blackened, especially at base; soral scales extremely rare, peltate, 0.1 mm wide, light brown with fimbriate margin; sori slightly oval; reproductive status uncer-

tain, specimen with juvenile sporangia and mature sporangia open with no spores present.

Additional collection: Mexico, Veracruz, Altotonga, 1938, *M. B. Foster 14* (US!).

Discussion.—The type of *Pl.* ×*melanoneuron* was originally a paratype of *Polypodium sordidulum*. However, it differs in several characters that point to a separate origin as the hybrid of *Pleopeltis fallax* (Fig. 2S–U) and *Pl. crassinervata* (Fig. 2A) (see Table 6). It resembles *Pl.* ×*sordidula* in its irregular blade division and both lanceolate and round scales on the adaxial and abaxial laminar surfaces. The evident lateral veins, blackened at their bases, differ significantly from the obscure lateral veins of *Pl.* ×*sordidula* and point to *Pl. crassinervata*, with its black lateral veins, as its simple-bladed parent. The rhizome scales of *Pl.* ×*melanoneuron* are definitely lanceolate, bicolorous, and larger than those of *Pl.* ×*sordidula*, again pointing to *Pl. crassinervata* with its longer, lanceolate rhizome scales with wider pale margins than in *Pl. astrolepis*. The stipe in *Pl.* ×*sordidula* is flattened (from *Pl. astrolepis* with its strongly flattened stipe), whereas in *Pl.* ×*melanoneuron* the stipe is terete (since both *Pl. fallax* and *Pl. crassinervata* have terete stipes). The rachis scales in *Pl.* ×*melanoneuron* are lanceolate and non-comose (similar to *Pl. crassinervata*), whereas in *Pl.* ×*sordidula* they are round and comose (both *Pl. fallax* and *Pl. astrolepis* have comose rachis scales, round in the former and lanceolate and round in the latter). The oblanceolate blade of *Pl.* ×*melanoneuron* is acute at the apex and has scales with dark, non-clathrate centers, whereas *Pl.* ×*sordidula* has a linear-lanceolate blade with an acuminate apex and scales with dark, semiclathrate centers.

Acknowledgments

We thank Thomas Wendt, Michael Nee, and W. H. Wagner Jr. for useful discussions, and Rupert Barneby for his kind assistance with the Latin diagnoses. Figures 1A, B, F–H, M, N, 2A, L–N, S–U were drawn by H. Fukuda; the other figures and the plate layouts were prepared by Bobbi Angell. The drawings and publication were supported in part by the Joann Wolfe Ward Memorial Research Fund.

Literature Cited

Anthony, N. C. and E. A. Schelpe. 1985. ×*Pleopodium*—a putative intergeneric fern hybrid from Africa. Bothalia 15:555–559.

Evans, A. M. 1963. New chromosome observations in the Polypodiaceae and Grammitidaceae. Caryologia 16:671–677.

Lellinger, D. B. 1985. *A field manual of the ferns & fern-allies of the United States & Canada*. Washington, D.C.: Smithsonian Institution Press.

Mickel, J. T. and J. M. Beitel. Pteridophyte flora of the state of Oaxaca, Mexico. Mem. N.Y. Bot. Gard. (in press).

Proctor, G. R. 1977. *Flora of the Lesser Antilles. Vol. 2. Pteridophyta*. Jamaica Plains, Massachusetts: Arnold Arboretum.

———. 1985. *Ferns of Jamaica*. London: British Museum (Natural History).

Smith, A. R. 1981. Pteridophytes. In *Flora of Chiapas, Part 2*, ed. D. E. Breedlove. San Francisco: California Academy of Sciences.

———. 1985. *Pteridophytes of Venezuela, an annotated list*. Berkeley, California: published by author.

STOLZE, R. G. 1981. Ferns and fern allies of Guatemala. Fieldiana, Bot. n.s. 6:i–vii, 1–522.

TRYON, R. M. and A. F. TRYON. 1982. *Ferns and allied plants, with special reference to tropical America*. New York: Springer-Verlag.

VARESCHI, V. 1969. *Flora de Venezuela. Vol. 1. Helechos*. Caracas: Instituto Botanico.

WAGNER, W. H. JR. and F. S. WAGNER. 1975. A hybrid polypody from the New World tropics. Fern Gaz. 11:125–135.

WALKER, T. G. 1966. A cytotaxonomic survey of the pteridophytes of Jamaica. Trans. Roy. Soc. Edinburgh 66:169–237 + 5 pl.

———. 1973. Additional cytotaxonomic notes on the pteridophytes of Jamaica. Trans. Roy. Soc. Edinburgh 69(5):109–135.

WEATHERBY, C. A. 1922. The group of *Polypodium lanceolatum* in North America. Contr. Gray Herb. 65:3–14.

———. 1935. On certain Mexican and Central American ferns. Amer. Fern J. 25:52–59.

WENDT, T. 1980. Notes on some *Pleopeltis* and *Polypodium* species of the Chihuahuan Desert region. Amer. Fern J. 70:5–11.

1987 AIBS MEETING—CALL FOR PAPERS

The American Fern Society and the Botanical Society of America will meet with the American Institute of Biological Sciences at Ohio State University, Columbus, 9–13 August 1987. Members of the American Fern Society wishing to present a paper or poster may obtain abstract forms from the Program Chairman: Dr. Christopher H. Haufler, Department of Botany, University of Kansas, Lawrence, KS 66045.

A Fern Foray to the Hocking Hills will take place on Sunday, 9 August 1987. Cost: $21 per person, includes box lunch. Trip is limited to 45 people and will leave from the 12th Avenue (south side) of the Ohio Union at 8:00 a.m. and return at 6:00 p.m. The pteridophytes of the unglaciated areas south of Columbus will be studied in their natural habitat and will include especially those of the sandstone cliff faces and grottos. Hybrids will be seen in several genera: *Asplenium* ×*trudellii*, *Cystopteris* ×*wagneri*, and *Dryopteris* ×*neo-wherryi*, as well as the remarkable grotto gametophytes of *Vittaria* and *Trichomanes*. A number of threatened and endangered species on the Ohio list will be observed, but collecting of only common species will be permitted. Leaders are R. James Hickey, W. H. Wagner Jr., and Charles R. Werth. For more information, contact Wagner at (313) 764-1484.

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Flavonoids and Spores of *Platyzoma microphyllum*, an Endemic Fern of Australia

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This is the first report of flavonoid aglycones in the Australian endemic fern, *Platyzoma microphyllum* R. Br. These are deposited on the leaves as filamentous crystals from glandular trichomes (Barthlott & Wollenweber, 1981). Such lipophilic deposits have been identified on leaves of several genera of the Pteridaceae. They occur in almost all species of *Pityrogramma*, many in *Notholaena*, some in *Cheilanthes*, and a few in *Pellaea* and *Pterozonium* (Wollenweber, 1978). They have been designated as "wax" or "ceraceous indument" in taxonomic literature and as "farinose exudate" or merely as "farina" in phytochemical literature. The term "wax" is incorrect as this material is not a true wax in chemical terms. Extensive studies of the chemical composition of such exudates have revealed that they are usually a mixture of flavonoid aglycones (Wollenweber, 1978), sometimes with considerable amounts of terpenoids (Wollenweber et al., 1982; Arriaga-Giner & Wollenweber, 1986). As part of our continuing studies of the flavonoid excretions (Wollenweber, 1985) we have made a detailed analysis of *Platyzoma microphyllum*. The species is remarkable for the incipient heterosporous condition (A. Tryon, 1964; A. Tryon & Vida, 1967; Duckett & Pang, 1984) and production of filamentous male gametophytes as well as largely archegoniate spatulate gametophytes.

MATERIAL AND METHODS

Specimens were collected at Nicotine Creek, southwest of Mareeba, Queensland, Australia (*R. & A. Tryon 7342*, GH; Wollenweber Herbarium, Darmstadt). The plants were growing in dry *Eucalyptus* scrub, an unusual habitat for ferns (Fig. 1). There were many large clumps growing among sparse grass, on sand that was damp below the surface. A xeric habitat is often characteristic of other species of the Pteridaceae with flavonoid aglycones.

Leaves were washed with acetone to dissolve the lipophilic exudate and the concentrated solution was chromatographed over polyamide. Two flavonoids crystallized from the relevant fractions as fine yellow needles. They were identified by their UV and mass spectra, and these identifications were confirmed by direct comparisons with authentic samples. Six minor flavonoids were identified by co-chromatography with markers (for details of experimental routine procedures see, e.g., Wollenweber et al., 1985).

Results

The spores are of two sizes, with the larger ones 162–190 μm and usually 16 per sporangium. The small spores are 65–105 μm and usually 32 per sporangium. The size differences are apparent in the sample illustrated (Fig. 3). A granulate deposit often covers the reticulate surface in both spore types. There are a series of parallel ridges in the equatorial region of the large spores (Fig. 4) that are absent in the small ones. The development of morphologically distinct gametophytes from the two spore types and origin of heterospory were examined by Duckett and Pang (1984).

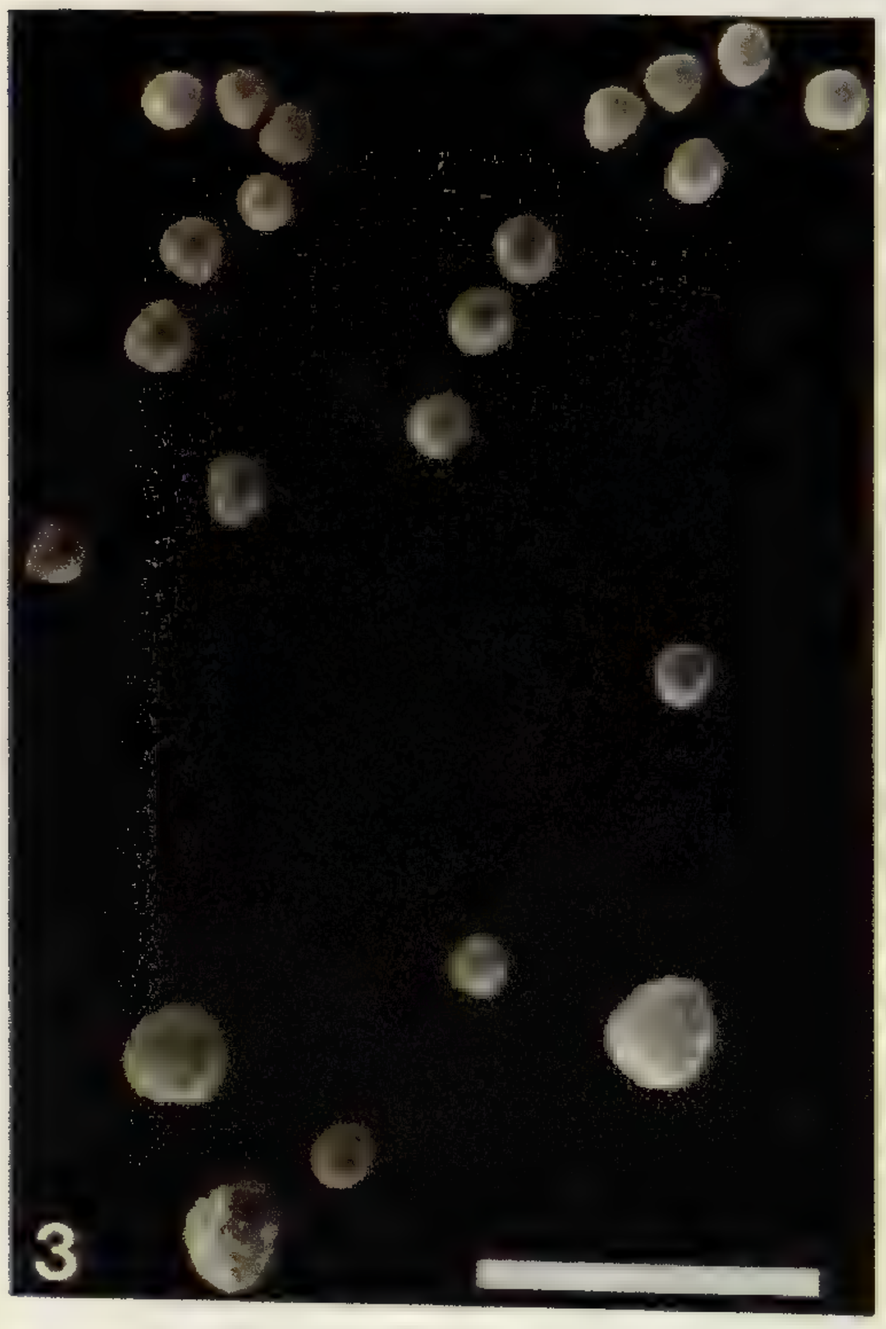
The leaves have indeterminate growth with two rows of coriaceous, pouch-like pinnae adjacent to the rachis (Fig. 2). Two- or three-celled, capitate glands are abundant on the pinnae, which usually have accumulations of yellowish exudate on the surface. Freshly collected specimens have a characteristic scent and, when pressed, leave an oily stain on paper. The odor and stain might be due to the presence of essential oils of some kind. The flavonoid aglycones that cause the yellow color of the leaf exudate were analyzed.

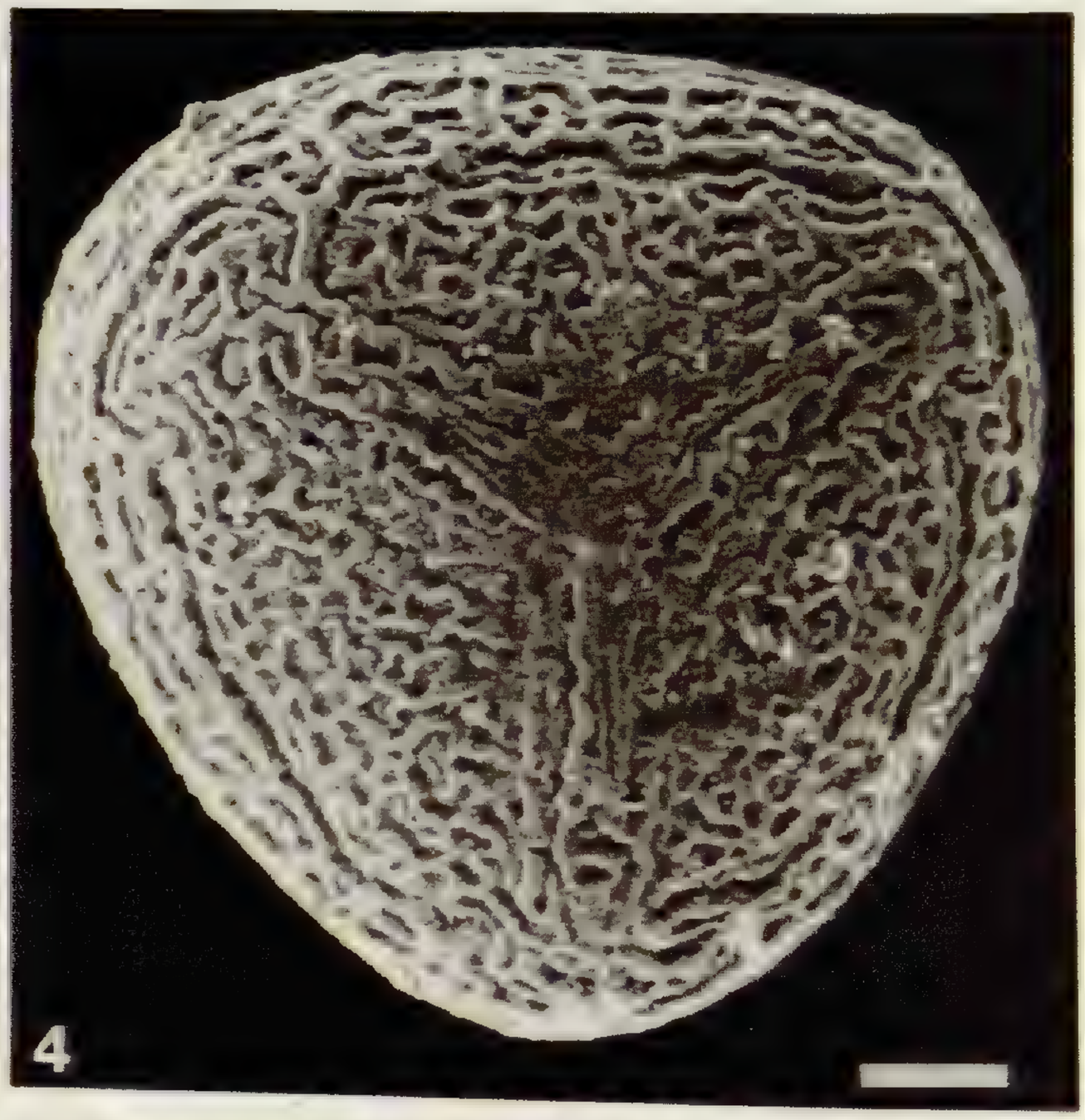
Two major flavonoids were obtained in crystalline form. They were found to be 2′,6′-dihydroxy-4′-methoxy chalcone (Fig. 5a) and 2′,6′-dihydroxy-4′,5′-dimethoxy chalcone (pashanone, Fig. 5b). As minor components, we identified the flavanone pinocembrin-7-methyl ether (pinostrobin, Fig. 5c) and the flavanols galangin-7-methyl ether (izalpinin, Fig. 5d), galangin-3,7-dimethyl ether (Fig. 5e), kaempferol-7-methyl ether (rhamnocitrin, Fig. 5f), kaempferol-3,7-dimethyl ether (kumatakenin, Fig. 5g), and kaempferol-3,7,4′-trimethyl ether (Fig. 5h). Some further trace constituents could not be identified, due to lack of material.

The 2′,6′-dihydroxy-4′-methoxy chalcone is a typical component of yellow or orange leaf exudates in *Pityrogramma* species (except *P. triangularis*; Wollenweber & Dietz, 1980). Several species of *Cheilanthes* and *Notholaena* also produce this chalcone (Wollenweber, 1982a). The rare 2′,6′-dihydroxy-4′,5′-dimethoxy chalcone, pashanone, occurs jointly with the former chalcone as major constituents of the leaf exudate of *Onychium siliculosum* (Desv.) C. Chr. (Wollenweber, 1982b). Pinocembrin-7-methyl ether is assumed to be an artifact, derived from the first mentioned chalcone by cyclization. The methylated flavonols (Figs. 5d–h) are common constituents of the ceraceous indument in *Cheilanthes* and *Notholaena* species and in some varieties of *Pityrogramma triangularis* (Smith, 1980). They were also encountered, in trace amounts, in the thin epicuticular layer on glaucous leaflets of several *Pellaea* species (Wollenweber, 1982a).

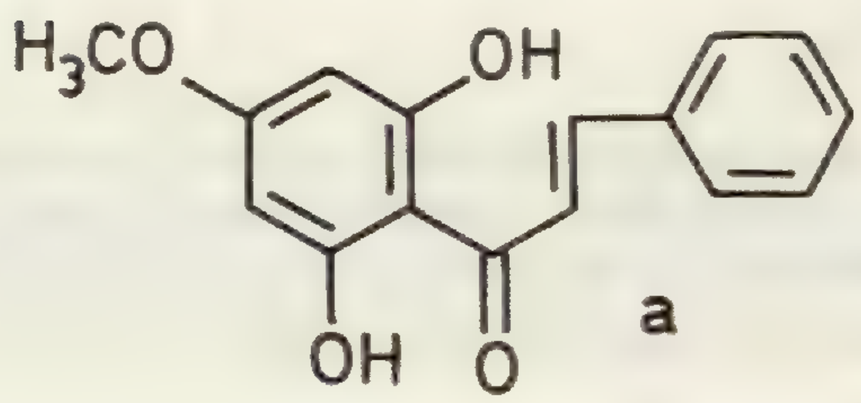
Discussion

The systematic position of this fern has long been in question, due to its unusual leaf morphology, incipient heterosporous condition, and two forms of gametophyte. It was initially placed in the Gleicheniaceae by Robert Brown in 1810 or considered a separate family, Platyzomataceae, in the Gleicheniales (Nakai, 1950). It was treated as subfamily *Platyzomatoideae* in the Polypodiaceae





FIGS. 1–4. *Platyzoma microphyllum*. FIG. 1. Three clumps of the plants with *Eucalyptus* trees in the background, near Mareeba, Queensland, Australia. FIG. 2. Part of filiform leaf with pouch-like pinnae, bar = 2 mm. FIG. 3. Small spores and three large ones below, bar = 500 μm. FIG. 4. Proximal face of large spore, parallel ridges in the equatorial region. Queensland, Australia, *Brass & White 64* (GH), bar = 25 μm.



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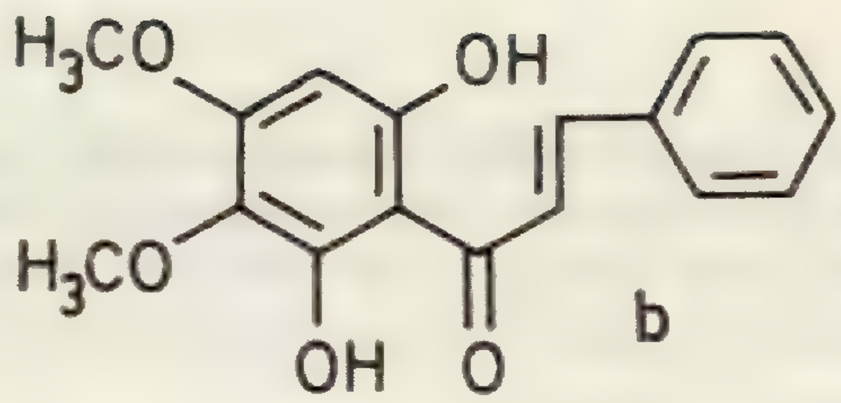

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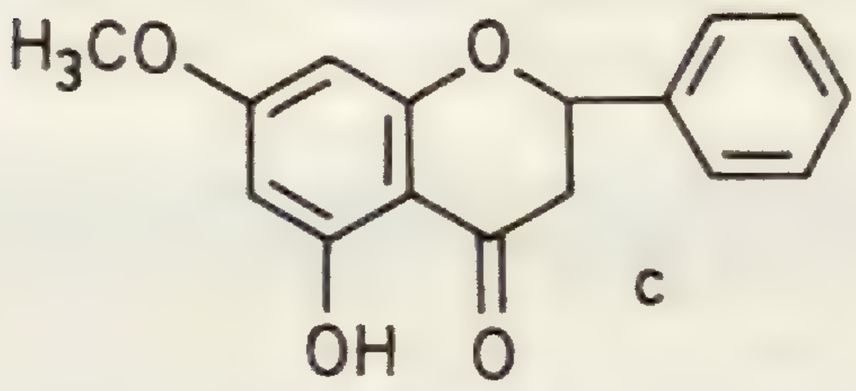

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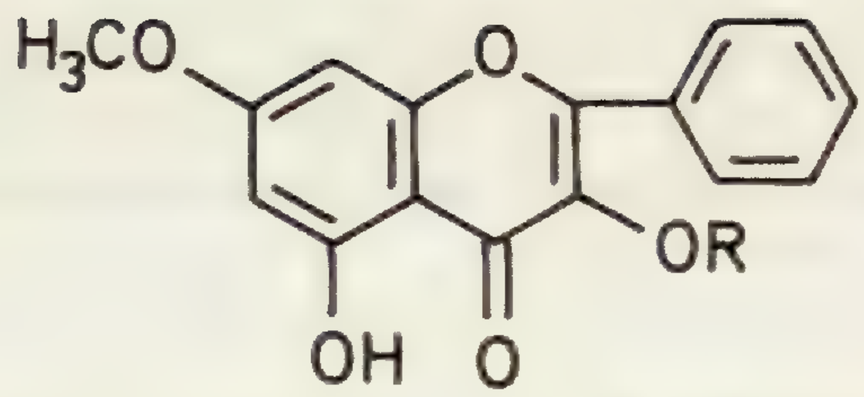
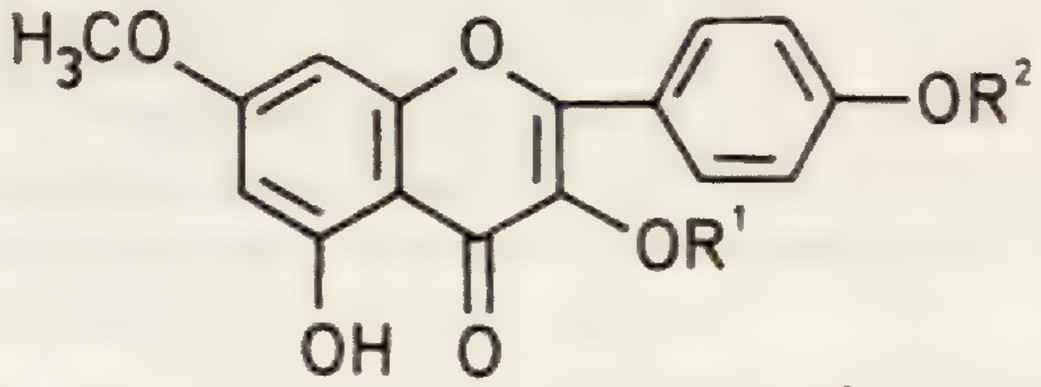


d : R = H

e : R = CH_3



f : $R^1 = R^2 = H$

g : $R^1 = CH_3$, $R^2 = H$

h : $R^1 = R^2 = CH_3$

FIG. 5. Flavonoid aglycones that cause the yellow color of the leaf exudate in *Platyzoma microphyllum*: a—2′,6′-dihydroxy-4′-methoxy chalcone, b—pashanone, c—pinostrobin, d—izalpinin, e—galangin-3,7-dimethyl ether, f—rhamnocitrin, g—kumatakenin, h—kaempferol-3,7,4′-trimethyl ether.

(A. Tryon 1961, 1964), and in the tribe *Platyzomateae* in the Pteridaceae (R. & A. Tryon, 1982). Flavonoid aglycones that are excreted and accumulated on the leaf surface have so far been reported for representatives of the genera *Pityrogramma* and *Pterozonium* (tribe Taenitideae), for *Cheilanthes*, *Notholaena*, *Pellaea*, *Negripteris*, *Sinopteris*, and *Onychium* (tribe Cheilantheae), and for *Adiantum* (tribe Adianteae) (Wollenweber, 1979).

Several characteristics of the plants as the medulated protostele, sporangium morphology, and especially the chromosome report of $n = 38$ suggest connections with the Schizaeaceae (A. Tryon & Vida, 1967). The incipient heterosporous condition, known in several unrelated families as the Selaginellaceae, Marsileaceae, and Salviniaceae, has undoubtedly developed independently in *Platyzoma*. The presence of flavonoid aglycones, such as those forming the lipophilic leaf exudate in *Platyzoma microphyllum*, are thus far known only in the Pteridaceae. This supports its treatment in that family, while the unusual morphology, chromosome number, and heterosporous condition support recognition of the species in a separate tribe.

ACKNOWLEDGMENTS

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Literature Cited

Arriaga-Giner, F. J. and E. Wollenweber. 1986. 6α-Acetoxy-16β, 22-dihydroxyhopan 24-oic acid, a triterpene from the fern *Notholaena candida* var. *copelandii*. Phytochemistry 25:735–737.

Barthlott, W. and E. Wollenweber. 1981. Zur Feinstruktur, Chemie und taxonomischen Signifikanz epicuticularer Wachse und ähnlicher Sekrete. Trop. Subtrop. Pflanzenwelt (Akad. Wiss. Lit. Mainz) 32:35–97.

Duckett, J. G. and W. C. Pang. 1984. The origins of heterospory: a comparative study of the sexual behaviour in the fern *Platyzoma microphyllum* R. Br. and the horsetail *Equisetum giganteum* L. J. Linn. Soc., Bot. 88:11–34.

Nakai, T. 1950. A new classification of Gleicheniales. Bull. Natl. Sci. Mus. 29:1–71.

Smith, D. M. 1980. Flavonoid analysis of the *Pityrogramma triangularis* complex. Bull. Torrey Bot. Club 107:134–145.

Tryon, A. F. 1961. Some new aspects of the fern *Platyzoma microphyllum*. Rhodora 63:91–102.

———. 1964. *Platyzoma*—A Queensland fern with incipient heterospory. Amer. J. Bot. 51:939–942.

——— and G. Vida. 1967. *Platyzoma*: A new look at an old link in ferns. Science 156:1109–1110.

Tryon, R. M. and A. F. Tryon. 1982. *Ferns and allied plants, with special reference to tropical America*. New York: Springer-Verlag.

Wollenweber, E. 1978. The distribution and chemical constituents of the farinose exudates in gymnogrammoid ferns. Amer. Fern J. 68:13–28.

———. 1979. Einige Neufunde externer Flavonoide bei amerikanischen Farnen. Flora 268:138–145.

———. 1982a. Flavonoid aglycones as constituents of epicuticular layers in ferns. In *The plant cuticle*, ed. D. F. Cutler et al. Linn. Soc. Symp. Ser. 10:215–224.

———. 1982b. The occurrence of flavanones in the farinose exudate of the fern *Onychium siliculosum*. Phytochemistry 21:1462–1464.

———. 1985. Chemotaxonomic studies on cheilanthoid ferns. Taxon 34:356–357.

——— and V. H. Dietz. 1980. Flavonoid patterns in the farina of goldenback and silverback ferns. Biochem. Syst. Ecol. 8:21–33.

———, ———, G. Schilling, J. Favre-Bonvin, and D. M. Smith. 1985. Flavonoids from chemotypes of the goldback fern, *Pityrogramma triangularis*. Phytochemistry 24:965–971.

———, P. Ruedi, and D. S. Seigler. 1982. Diterpenes of *Cheilanthes argentea*. Z. Naturf. 37c: 1283–1285.

American Fern Journal 77(1):33–35 (1987)

A New Species of *Danaea* from Peru

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Current studies for the "Pteridophytes of Peru," in which I am collaborating with Dr. Rolla Tryon of Harvard University, have already yielded some fascinating discoveries worthy of special note. The first of these to come to my attention was a new species of *Danaea*, which is hereunder described.

6106 **Danaea oblanceolata** Stolze, sp. nov. (Figs. 1–3).—TYPE: Peru, Dept. Pasco (as Junín), Cahuapanas, on Río Pichis, *Killip & Smith 26777* (US, frag. F).

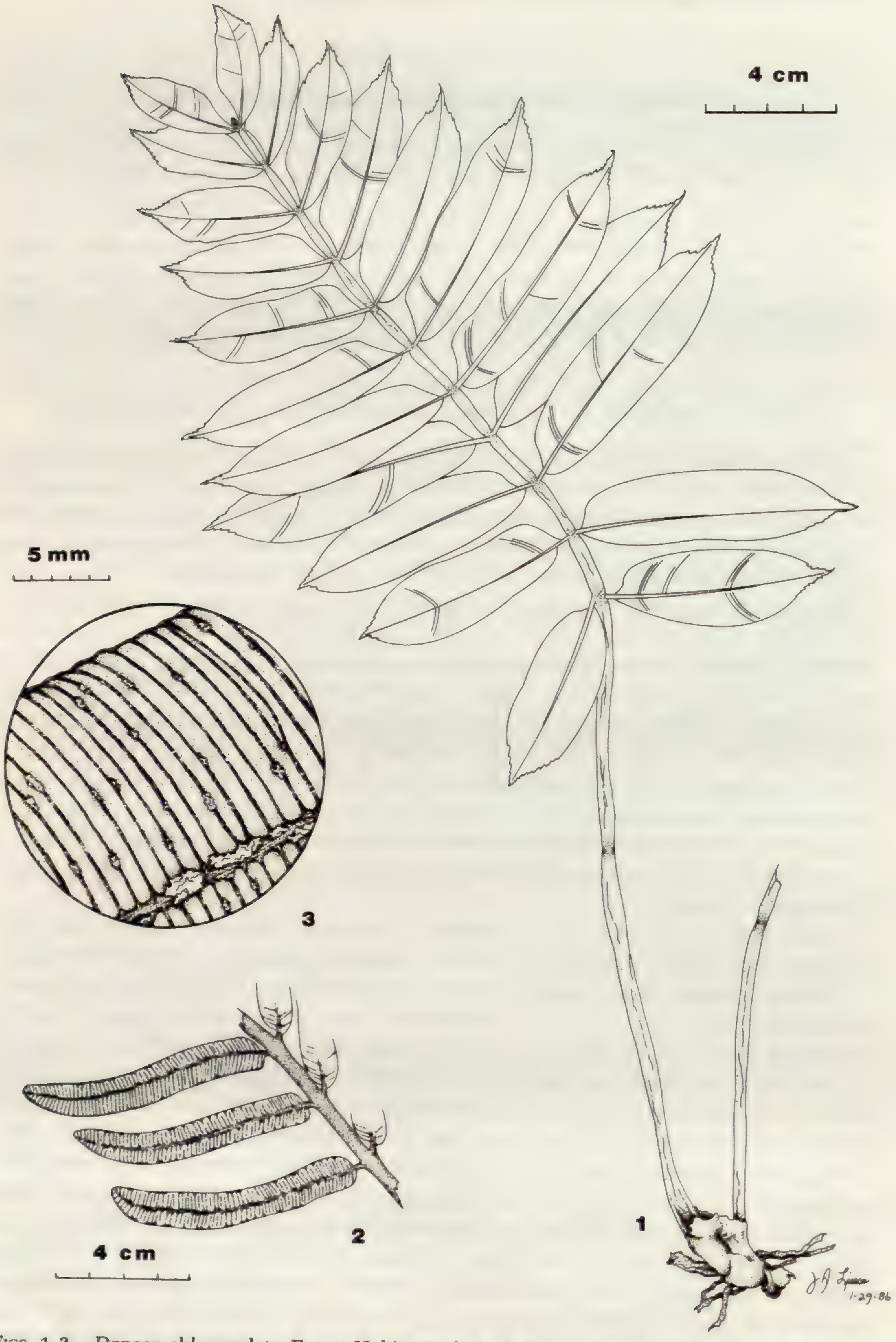
Folia sterilia 40–50 cm longae, 13–18 cm latae, ad apices prolificantia; petiolus 1–2-nodosis; pinnae 10–12-jugae, late oblanceolatae, usque ad 11 cm longae et 2.8 cm latae, ad apicem acuminatae et serratae abrupte terminantes; venae plerumque simplices, autem interdum geminae vel 1-furcatae. Pinnae fertiles cerca 12-jugae, usque ad 8 cm longae et 1 cm latae, ad apicem obtusae.

Sterile leaves 40–50 cm long, 13–18 cm broad, apical segment replaced by a proliferous bud; petiole with 1–2 nodes, moderately to abundantly scaly; rachis narrowly alate; pinnae 10–12 pairs, mostly short-stalked, oblong to (more commonly) broadly oblanceolate, larger ones 7–11 cm long and 2–2.8 cm broad, inequilateral at base, narrow and rounded to cordate basiscopically, broader and cuneate acroscopically, terminating abruptly in an acuminate and serrate apex, abaxial surface amply provided with minute, dark brown scales; veins commonly simple, but sometimes paired at origin or forked. Fertile pinnae 12–14 pairs, larger ones 7–8 cm long and 0.8–1 cm broad, short-stalked, the apex obtuse.

Terrestrial in dense forests, 0–500 m, thus far known only from Peru: Depts. Pasco and Ucayali.

Additional collections: PERU. **Pasco**: Oxapampa, Palcazu Valley, Iscozacin, *R. Foster 9466* (MO), *10049* (F). **Ucayali**: Vicinity of Aguaytia, *Croat 20938* (MO).

This is perhaps most closely related to *D. alata* Sm., of the West Indies and Venezuela, especially in that both species have predominantly simple veins. However, in *D. oblanceolata* pinnae are fewer and relatively shorter and broader, and most of them are broadest well above the middle, where the margins then curve abruptly to a short-acuminate apex. In *D. alata*, as in all members of the *D. moritziana* complex, pinnae are broadest at or near the middle, from whence they taper gradually to a moderately acuminate or attenuate apex. *Danaea moritziana* Presl, found rather frequently in Venezuela, Colombia and Peru, is further distinguished from *D. oblanceolata* in the predominantly forked veins (only occasionally simple or paired at base). Moreover, it is possible that the Central American *D. cuspidata* and one or two West Indian species are synonymous with *D. moritziana*. A number of taxa with pinnae under 2.5 cm broad were separated by Underwood (Bull. Torrey Bot. Club 29:669–679. 1902), merely on the degree of forking and spacing of veins, an apparently inconsistent char-



FIGS. 1–3. *Danaea oblanceolata*. FIG. 1. Habit, sterile leaf, showing apical proliferous bud. FIG. 2. Portion of rachis and three fertile pinnae. FIG. 3. Section of sterile pinna, abaxial side, with predominantly simple veins, amorphous scales on costa and veins.

acter correlated rarely or not at all by other features; hence, a comprehensive revision of the genus is needed to clarify the taxonomy.

In all the specimens of *D. oblanceolata* thus far examined, a proliferous bud has been found at the apex of the sterile leaves. This character has been observed in three of the other five species of the genus in Peru; it is frequently found in *D. humilis* Moore and *D. trichomanoides* Moore, and occasionally in *D. moritziana*. Apical proliferations are also found in several other West Indian and Central American species. Although this is an interesting feature, it is usually not a diagnostic one, for in most species with which I am familiar, it is not fully constant.

REVIEWS

"*A monograph of the fern genus* Pyrrosia *(Polypodiaceae),*" by P. Hovenkamp. 1986. xiii + pp. 1–280 including 6 pp. of photos and 37 figs. "*The* Pyrrosia *species formerly referred to* Drymoglossum *and* Saxiglossum *(Filicales, Polypodiaceae),*" by W. J. Ravensberg and E. Hennipman. 1986. pp. 281–310, 4 figs. Leiden Botanical Series, Vol. 9. Available from E. J. Brill, P.O. Box 9000, 2300 PA Leiden, Netherlands, 120 guilders, approx. $53.33. ISBN 90-04-08065-1.

Pyrrosia is among the most abundant of Old World epiphytes in both individuals and species. In his 1947 Genera Filicum, Copeland estimated 100 *Pyrrosia* species without including *Drymoglossum*, a number now reduced to a conservative 51 by Hovenkamp, Ravensberg, and Hennipman.

Although combined in a single volume, the monograph has two sections with different authors; the pagination is continuous, and all species are included in one key, but the indices to collections and taxonomic names are not integrated. The much smaller second portion by Ravensberg and Hennipman treats six species of four different affinities, grouped only because the six were often referred to *Drymoglossum* and *Saxiglossum*, both reduced to *Pyrrosia*. The main treatment dealing with 45 species, by Hovenkamp, also has detailed sections on morphology, phylogeny, and biogeography. Altogether it is a very thorough and impressive accumulation of information. The nomenclature, descriptions, and distributions are authoritative and very useful.

However, the chapter on phylogeny was not easy for me to understand, and I found the premise, that *Pyrrosia* and *Platycerium* are sister genera, unlikely. Such would require that an immediate ancestor of *Platycerium* was also the ancestor of all extant *Pyrrosia*. A more attractive hypothesis is that *Pyrrosia* is considerably older than the highly specialized *Platycerium*, and had already diversified into plural species we would unhesitatingly classify as *Pyrrosia* if extant today, and that one of these early *Pyrrosia* species was the source of *Platycerium*.

Perhaps the sister genus misconception has led to further misconceptions. I believe the immediate ancestor of *Pyrrosia* was very similar to other polypods, sharing a creeping rhizome with internal sclerenchyma strands, peltately at-

tached paleae, fronds articulate to phyllopodia, veins anastomosing with regular areoles, hydathodes present, etc. But instead of allowing for a common origin with other Polypodiaceae, Hovenkamp (pp. 100–102) presents a case for a relationship of *Pyrrosia* with *Dipteris*, a genus with a radically different groundplan and with only a very remote affinity, at best, to the polypods.

On the basal branch of the *Pyrrosia* cladogram (p. 95) is the *P. africana* group consisting of two African species that completely lack rhizome sclerenchyma, have ±irregular venation, pseudopeltate paleae, vestigially articulate fronds, no woolly rays of stellate hairs, a total absence of hydathodes in one, the other with a unique modification of the annulus. These two species appear to me to be reduced derivatives of the *P. porosa* group which they closely resemble in overall morphology and which contains two other African species with reduction characters transitional to these in rhizome sclerification and laminar indument.

A further argument against the *P. africana* group being relictual in *Pyrrosia* is phytogeographical. The genus would probably have reached tropical America if, as hypothesized, it had an early origin in what is now Africa; by far the greatest diversity in the genus is now in the eastern Himalayas, southeast Asia, and Malesia.

However, it is only because Hovenkamp gives us so very much information that it is easy to debate with him about the phylogeny of his genus. This is a positive, not a negative aspect, and not a detraction from the great value of the work as a whole.—M. G. PRICE, Herbarium, North University Building, University of Michigan, Ann Arbor, MI 48109.

"*Index of Thelypteridaceae*," by J. W. Grimes and B. S. Parris. 1986. iv + 50 pp. Royal Botanic Gardens, Kew. Available from B. Parris, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, England. £7.25 (incl. postage and handling). ISBN 0 947643 03 6.

This is an alphabetical listing by specific epithet (accepted names and synonyms) of all species of *Thelypteris* s.l., with citation of original genus and current disposition of the name as recognized by authorities in the group. There is also a selected bibliography of 65 references to major literature concerning the family. No new combinations are included. The list will be useful primarily to curators of herbaria who wish to arrange their specimens according to recent reclassifications, primarily by Holttum, and also as a reference for specialists and floristicians working with the family. I found the work to be relatively free of errors, but a brief search uncovered several overlooked basionyms and incorrect attributions of current names.—ALAN R. SMITH, Department of Botany, University of California, Berkeley, CA 94720.

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Argyrochosma, a New Genus of Cheilanthoid Ferns

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The group of fern species related to *Notholaena nivea* (Poir.) Desv. has long been a source of taxonomic contention. In the 183 years since *N. nivea* was first described (as *Pteris nivea* Poir.), members of this alliance have been assigned to no fewer than ten genera, including *Acrostichum, Cheilanthes, Gymnogramma,* and several others no longer in use. Detailed morphological and anatomical investigations leave no doubt that these species are cheilanthoid ferns in the strict sense (Tryon & Tryon, 1982), and most recent authors place this group in either *Notholaena* or *Pellaea.* Rolla Tryon, Maxon, and others who favor placement in *Notholaena* (as typified by *N. trichomanoides*) emphasize two characters that seem to indicate an affinity to that genus: 1) the presence of a farinose indument on the abaxial leaf surface in most species and 2) the absence of a pseudoindusium formed by a modified leaf margin. Those who classify the *N. nivea* complex with *Pellaea* (i.e., Prantl, Christensen, and Morton) stress similarities in spore ornamentation, sporangial distribution and leaf architecture. Despite disagreement over the relative importance of different morphological traits, both groups of pteridologists seem to recognize the *N. nivea* complex as a natural alliance, and the sectional name *Argyrochosma* (proposed by J. Smith in 1841) has often been applied to it regardless of generic assignment.

Copeland and Weatherby recommended a different approach to the taxonomic problems raised by the *N. nivea* group. In *Genera Filicum,* Copeland (1947, p. 70) stated that "The group placed under *Pellaea* in Christensen's *Index,* p. XL, as sect. *Argyrochosma,* typified by *P. nivea* (Poir.) Prantl, has no proper place in the genus. . . . It seems to be a proper generic entity, without a name as such." In a letter to Morton dated March, 1949 (quoted in Morton, 1950, pp. 249–250), Weatherby was even more specific. He stated that "this is one of the two groups (and the better of the two) which I can see clearly as a segregate genus. If to the group of *N. nivea, N. dealbata, N. fendleri,* et cetera, you add *N. Jonesii, N. Lumholtzii, Pellaea microphylla,* and *P. formosa,* you get a coherent and, I think, natural group, which as a genus, should bear the name *Argyrochosma* (J. Smith)." Unfortunately, neither Copeland nor Weatherby lived to complete his study, and subsequent authors have not followed their recommendations.

Ongoing biosystematic investigations of *Pellaea, Notholaena,* and the *N. nivea* complex (Windham, unpubl.) serve to reinforce the idea that *Argyrochosma* is a natural (monophyletic) group worthy of generic recognition. Tryon and Tryon (1982) pointed out that sections *Argyrochosma* and *Notholaena* (the latter typified by *N. trichomanoides*) are distinct in terms of rhizome scales, leaf architecture, sporangial distribution, and spore morphology. These taxa also show consistent differences in chromosome number, gametophyte morphology, chemical composition of the farinose indument, and patterns of variability at conservative enzyme loci (Windham, 1986). Each of these characters indicates a close rela-

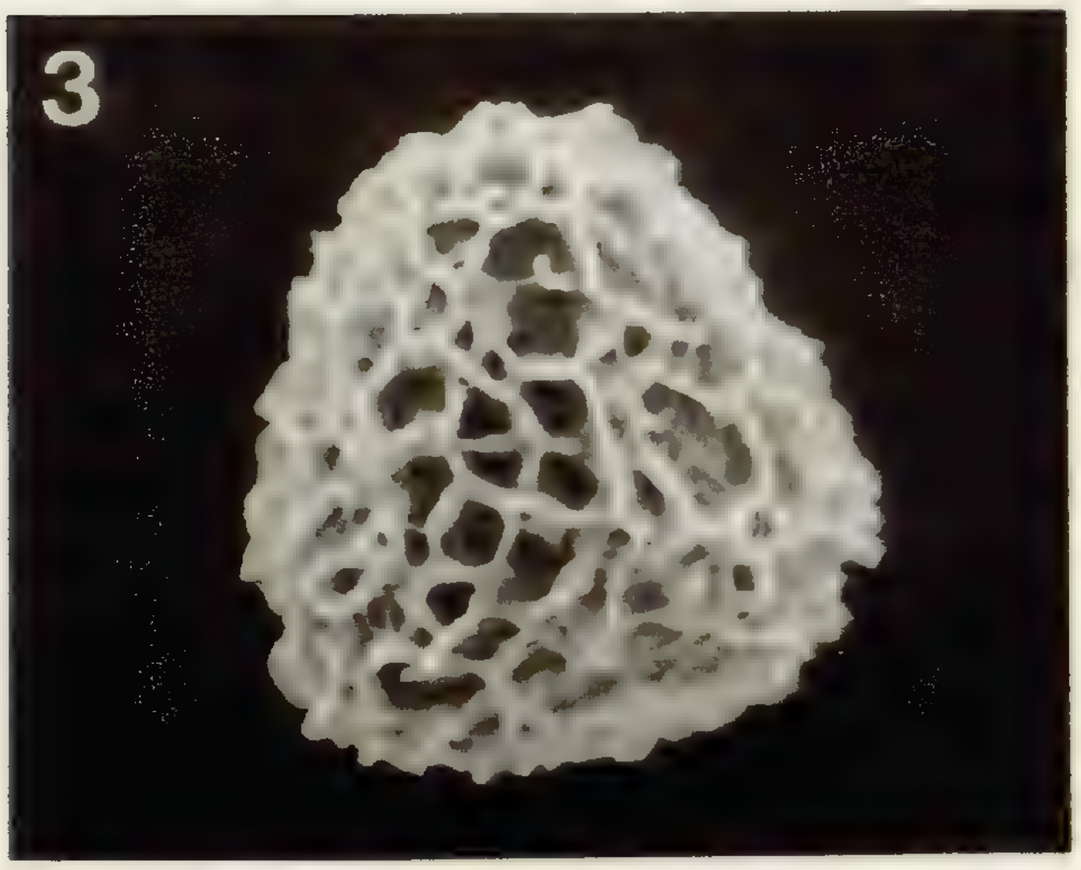
tionship between *Argyrochosma* and *Pellaea* sect. *Pellaea*, suggesting that these may be sister groups in a phylogenetic sense. However, the species of *Argyrochosma* exhibit a chromosome base number ($\bar{x} = 27$) unique among cheilanthoid ferns, and the two groups are easily distinguished using a combination of morphological features including rhizome scales, segment size and leaf dissection, nature of the leaf margin, and the occurrence of a farinose indument. The unique chromosome base number of *Argyrochosma* is here interpreted as a synapomorphy supporting the monophyletic origin of the group, and I concur with Copeland and Weatherby that *Argyrochosma* should be accorded generic rank among the cheilanthoid ferns (included in the family Adiantaceae).

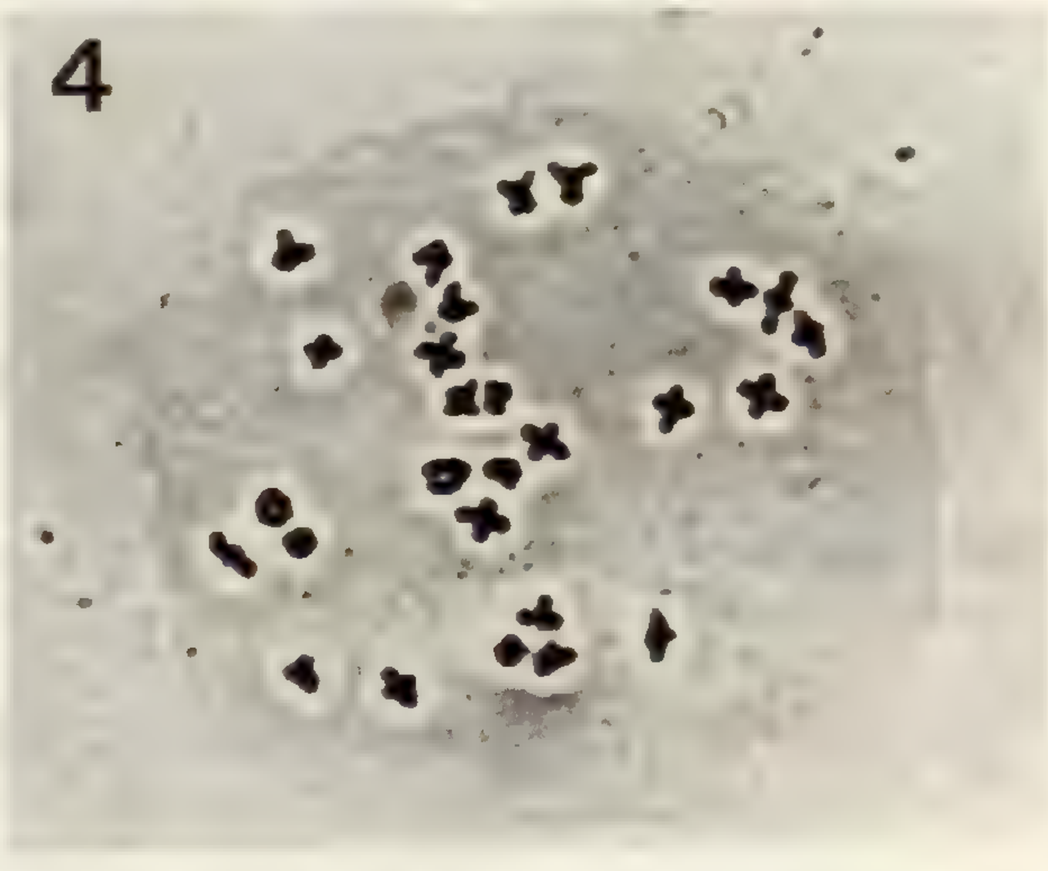
My comparative study of *Pellaea*, *Notholaena*, and *Argyrochosma* is nearing completion, but this detailed work is unlikely to be published prior to deadlines established for several new floristic manuals. Therefore, to facilitate the treatment of *Argyrochosma* in the *Flora of North America*, *Flora of California*, and *The ferns and fern allies of Arizona* (Windham & Yatskievych, in prep.), I herewith describe the genus and make nomenclatural combinations for the sixteen species currently included in it.

Argyrochosma (J. Smith) Windham, stat. nov.—*Notholaena* sect. *Argyrochosma* J. Smith, J. Bot. (Hooker) 4:50. 1841.—Lectotype (chosen by Christensen, 1906, Ind. Fil., p. XL): *Pteris nivea* Poir. [*Argyrochosma nivea* (Poir.) Windham].

Rhizome compact, short-creeping, erect to more or less decumbent, bearing scales and many fibrous roots. Rhizome scales thin, light brown to reddish brown, concolorous, up to 1 cm long, linear to lanceolate with an acuminate tip, entire to minutely denticulate. Leaves monomorphic, clustered, up to 40 cm long. Petiole terete to very shallowly sulcate, shorter than to slightly longer than the lamina, with a single vascular bundle; castaneous, atropurpureous, or blackish in color; glabrous, glaucous, sparsely ceraceous, or bearing small widely scattered scales or trichomes. Lamina imparipinnate (Fig. 1), linear-lanceolate, ovate or deltate; bipinnate to pentapinnate at the base, with up to 15 pairs of subopposite or alternate pinnae; coriaceous or (rarely) herbaceous, the upper surface glabrous or sparsely ceraceous, the lower glabrous or usually densely white (rarely yellow) ceraceous. Rachis similar to the petiole but occasionally flexuous. Pinnae lanceolate to deltate, generally remote, divided into numerous ultimate segments. Segments small, oblong to roundish or cordate, entire to shallowly lobed, petiolulate or (rarely) sessile; segment margins unmodified, rarely reflexed to protect sporangia. Veins free, 1- or 2-forked, the unmodified ultimate branches bearing sporangia for much of their length (Fig. 2). Sporangia with 64 or 32 spores. Spores trilete, light to dark brown, with cristate (Fig. 3) or rugose surfaces. Gametophytes usually cordate with wide notches, symmetrical and glabrous (lacking farina-producing trichomes). Chromosome number: x = 27 (Fig. 4).

Distribution.—A strictly American genus of approximately 20 species occupying rupestral or (rarely) terrestrial habitats from near sea level to an elevation of 4200 m in the Andes. Ranging from Missouri, Wyoming, and California to Chile (including the Juan Fernandez Islands), Argentina, and the highlands of southeastern Brazil. There is a large geographic gap between the North and South





FIGS. 1–4. Characteristics of the genus *Argyrochosma*. 1. Whole plant of *Argyrochosma nivea* (*Correll & Smith P743*, GH) showing habit and imparipinnate leaf architecture, × ⅓. 2. Leaf from the same individual showing sporangia distributed along the veins for much of their length, × 2. 3. Typical cristate spore of *A. formosa* (*Windham et al. 551, KANU*), × 750. 4. Meiotic chromosome squash of *A. delicatula* (*Windham et al. 482, KANU*) showing 27II, × 1000.

American elements of the genus (only *A. incana* is found in Central America and the West Indies), with the greatest diversity of species occurring in the highlands of central and northern Mexico.

ENUMERATION OF SPECIES (AND MAJOR SYNONYMS)

1) **Argyrochosma chilensis** (Fée & Remy) Windham, comb. nov.—*Cincinalis chilensis* Fée & Remy in Gay, Hist. Chile (Bot.) 6:497. 1853.—*Notholaena chilensis* (Fée & Remy) Sturm—*Pellaea chilensis* (Fée & Remy) C. Chr.

2) **Argyrochosma dealbata** (Pursh) Windham, comb. nov.—*Cheilanthes dealbata* Pursh, Fl. Amer. Sept. 2:671. 1814.—*Notholaena dealbata* (Pursh) Kunze—*Pellaea dealbata* (Pursh) Prantl.

Although this diploid taxon shows a strong morphological resemblance to the agamosporous triploid *A. limitanea* (Tryon, 1956), isozyme analyses indicate that the species, in its present form, was not involved in the origin(s) of that polyploid.

3) **Argyrochosma delicatula** (Maxon & Weath.) Windham, comb. nov.—*Notholaena delicatula* Maxon & Weath., Contr. Gray Herb. 127:7. 1939.

Preliminary isozyme data indicate that this is quite distinct from *A. incana* and should be maintained as a separate species despite the existence of a few intermediate individuals discussed by Maxon and Weatherby (1939) and Wollenweber (1984).

4) **Argyrochosma fendleri** (Kunze) Windham, comb. nov.—*Notholaena fendleri* Kunze, Farnkr. 2:87, t. 136. 1851.—*Pellaea fendleri* (Kunze) Prantl

5) **Argyrochosma formosa** (Liebm.) Windham, comb. nov.—*Allosorus formosus* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., V. 1:220 (Mex. Bregn. 68). 1849.—*Notholaena formosa* (Liebm.) R. Tryon—*Pellaea formosa* (Liebm.) Maxon.

6) **Argyrochosma incana** (Presl) Windham, comb. nov.—*Notholaena incana* Presl, Rel. Haenk. 1:19, t. 1, fig. 2. 1825.

Variations in flavonoid chemistry (Wollenweber, 1984) and spore size (Windham, unpubl.) within this widespread taxon suggest that it may include at least two distinct species.

7) **Argyrochosma jonesii** (Maxon) Windham, comb. nov.—*Notholaena jonesii* Maxon, Amer. Fern J. 7:108. 1917.—*Pellaea jonesii* (Maxon) Morton.

As currently defined, this species includes diploid and tetraploid cytotypes which tend to occupy different portions of the range. The type specimen, collected in Inyo County, California, probably represents the tetraploid.

8) **Argyrochosma limitanea** (Maxon) Windham, comb. nov.—*Notholaena limitanea* Maxon, Amer. Fern J. 9:70. 1919.—*Pellaea limitanea* (Maxon) Morton.

Both the typical form and var. *mexicana* (Maxon) Broun are agamosporous triploids which probably arose through different polyploidization events (Windham, unpubl.). If and when the diploid progenitors are identified, it may be necessary to recognize these varieties as distinct species.

9) **Argyrochosma lumholtzii** (Maxon & Weath.) Windham, comb. nov.—*Notholaena lumholtzii* Maxon & Weath., Contr. Gray Herb. 127:16. 1939.

10) **Argyrochosma microphylla** (Mett. ex Kuhn) Windham, comb. nov.—*Pellaea microphylla* Mett. ex Kuhn, Linnaea 36:86. 1869.—*Notholaena parvifolia* R. Tryon.

11) **Argyrochosma nivea** (Poir.) Windham, comb. nov.—*Pteris nivea* Poir., Encycl. 5:718. 1804.—*Notholaena nivea* (Poir.) Desv.—*Pellaea nivea* (Poir.) Prantl.

Although the typical form and var. *tenera* (Hook.) Griseb. both reproduce by means of agamospory, recent chromosome counts indicate that var. *nivea* is triploid while at least some individuals of var. *tenera* are diploid (Windham, unpubl.). The status of all four infraspecific taxa comprising *A. nivea* will need to be reassessed when additional genetic data become available.

12) **Argyrochosma pallens** (Weath. in R. Tryon) Windham, comb. nov.—*Notholaena pallens* Weath. in R. Tryon, Contr. Gray Herb. 179:78. 1956.

13) **Argyrochosma palmeri** (Baker) Windham, comb. nov.—*Notholaena palmeri* Baker, Hook. Icon. Pl. 17: t. 1678 & text. 1887.

14) **Argyrochosma peninsularis** (Maxon & Weath.) Windham, comb. nov.—*Notholaena peninsularis* Maxon & Weath., Contr. Gray Herb. 127:15. 1939.

15) **Argyrochosma pilifera** (R. Tryon) Windham, comb. nov.—*Notholaena pilifera* R. Tryon, Contr. Gray Herb. 179:79. 1956.

16) **Argyrochosma stuebeliana** (Hieron.) Windham, comb. nov.—*Pellaea dealbata* var. *stuebeliana* Hieron., Hedwigia 48:225, t. 12, fig. 15. 1909.—*Notholaena stuebeliana* (Hieron.) R. Tryon.

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Literature Cited

Copeland, E. B. 1947. *Genera Filicum*. Waltham, Mass.: Chronica Botanica Co.

Maxon, W. R. and C. A. Weatherby. 1939. Some species of *Notholaena*, new and old. Contr. Gray Herb. 127:3–17.

Morton, C. V. 1950. Notes on the ferns of the eastern United States (concluded). Amer. Fern J. 40: 241–252.

Tryon, R. M. 1956. A revision of the American species of *Notholaena*. Contr. Gray Herb. 179:1–106.

———— and A. F. Tryon. 1982. *Ferns and allied plants, with special reference to tropical America*. New York: Springer-Verlag.

Windham, M. D. 1986. Reassessment of the phylogenetic relationships of *Notholaena*. Amer. J. Bot. 73:742 (abstract).

Wollenweber, E. 1984. Exudate flavonoids of Mexican ferns as chemotaxonomic markers. Rev. Latinoamer. Quim. 15-1:3–11.

American Fern Journal 77(2):42-49 (1987)

Electrophoretic and Morphological Confirmation of Interspecific Hybridization between *Polystichum kruckebergii* and *P. munitum*

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The genus *Polystichum* (Dryopteridaceae) comprises from 160 (Tryon & Tryon, 1982) to 175 (Copeland, 1947) species and is nearly worldwide in distribution. Substantial morphological diversity exists within *Polystichum* (Barrington, 1985), and considerable taxonomic confusion has characterized *Polystichum* since its description in 1799. Systematic problems in *Polystichum* stem largely from extensive hybridization and allopolyploidy (Knobloch, 1976; Tryon & Tryon, 1982; Mickel in Barrington, 1985; D. Wagner in Barrington, 1985; W. Wagner in Barrington, 1985), which tend to obscure species boundaries and make morphological comparisons difficult. Furthermore, the production of interspecific sterile hybrids has created additional taxonomic confusion (Manton, 1950; Nakaike, 1973; W. Wagner, 1973; Daigobo, 1974; D. Wagner, 1979).

A prime example of the reticulate evolution typical of the genus (D. Wagner, 1979, in Barrington, 1985; W. Wagner in Barrington, 1985) is found in the *Polystichum* complex from western North America. This group consists of five diploid species, three once-pinnate (*P. imbricans*, *P. lonchitis*, and *P. munitum*) and two highly dissected (*P. dudleyi* and *P. lemmonii*). There are five tetraploids, *P. andersonii*, *P. braunii*, *P. californicum*, *P. kruckebergii*, and *P. scopulinum*; all but *P. braunii* incorporate various combinations of the diploid genomes discussed above (W. Wagner, 1973; D. Wagner, 1979). All of these species are restricted to western North America except *P. braunii* and *P. lonchitis*, which are circumboreal in distribution, and *P. scopulinum*, which also occurs sporadically in eastern North America. [Following D. Wagner (1979), *P. lemmonii* is considered distinct from the South American *P. mohrioides*.] *Polystichum setigerum*, reported to be a sexual hexaploid derived from *P. munitum* and *P. braunii* (D. Wagner, 1979), is also a member of this complex.

Several sterile hybrids among these species have been reported from North America, including *P. californicum* × *munitum* (Callan, 1972; W. Wagner, 1973), *P. braunii* × *munitum* (Alverson, unpubl.), *P. andersonii* × *munitum*, *P. californicum* × *dudleyi*, *P. dudleyi* × *munitum*, *P. lemmonii* × *munitum*, *P. lemmonii* × *scopulinum*, and *P. munitum* × *scopulinum* (W. Wagner, 1973), and *P. braunii* × *lonchitis* in Europe (Sleep & Reichstein, 1967). In addition, *P. braunii* has hybridized with the eastern North American *P. acrostichoides* (Thompson & Coffin, 1940; Barrington, 1986), and hybrids between *P. lonchitis* and *P. ac-*

rostichoides have also been reported (W. Wagner & Hagenah, 1954). Furthermore, both *P. braunii* and *P. lonchitis* have hybridized with the European species *P. aculeatum* and *P. setiferum* (reviewed by Sleep & Reichstein, 1967). In this paper we provide morphological and electrophoretic evidence for hybridization between *P. munitum*, a diploid, and *P. kruckebergii*, an allotetraploid whose presumed diploid progenitors are *P. lemmonii* and *P. lonchitis* (W. Wagner, 1973).

The putative hybrid plants under study are readily recognized as unusual; they possess moderately incised pinnae, which in nature are twisted relative to the axis of the rachis. The plants are medium-sized, with leaf blades of mature plants ranging from 35–42 cm by 5–6 cm; the plants are generally larger than the small, rock-dwelling polystichums, such as *P. kruckebergii*, but smaller than the large, forest-dwelling taxa, such as *P. munitum*. Close examination of the sori revealed abortive sporangia, as well as irregularly sized and shaped spores; many of the spores were shriveled and presumably abortive. Thus, the plants displayed features characteristic of interspecific hybrids (W. Wagner, 1968).

The putative hybrid between *P. munitum* and *P. kruckebergii* originated under an unusual set of geological circumstances. Typically, *P. munitum* and *P. kruckebergii* are not sympatric; *P. munitum* usually inhabits moist woods at lower elevations, and *P. kruckebergii* usually occurs at higher elevations, often on ultramafic substrates. The putative hybrids occur with *P. kruckebergii* and *P. munitum* at an elevation of approximately 1065 m on the lower slopes of Devil's Thumb in the Coal Creek drainage on the west side of the Cascades in Snohomish County, Washington. The plants grow at the base of a large glacial erratic of peridotite (an ultramafic mineral) that originated higher up on the mountain slope. This population of *P. kruckebergii* and the putative hybrids occur in an *Abies amabilis-Tsuga heterophylla* forest, at a much lower elevation than is typical of *P. kruckebergii*. This habitat and elevation are more typical of *P. munitum* in this region. *Polystichum lonchitis* was also present on a non-ultramafic outcrop 100 m away from the hybrid site and, instead of *P. munitum*, could conceivably be the once-pinnate parent of the putative hybrids. *Polystichum lonchitis* was therefore included in this study.

The origin of an interspecific hybrid can be extremely difficult to determine with certainty when only morphological criteria are employed, particularly in a plant group known for its phenotypic plasticity and environmentally induced variability (Barrington, 1985). Therefore, we utilized genetic markers in addition to morphological analyses to determine the origin of the putative hybrids.

Materials and Methods

Morphological data were obtained from pressed fronds of *P. munitum*, *P. kruckebergii*, and the putative hybrids collected at the hybrid locality. Vouchers were deposited at WS.

We electrophoretically examined the five putative hybrid plants, five individuals of *P. munitum*, and four individuals each of *P. kruckebergii* and *P. lonchitis* from the hybrid locality. Leaf material was collected in the field and stored in

plastic bags with wet paper towels under refrigeration until electrophoresis was conducted.

Electrophoretic procedures generally followed those of D. Soltis et al. (1983). Leaf tissue was prepared using the tris-HCl grinding buffer-PVP solution of D. Soltis et al. (1983); three grams of PVP were used per 25 ml of grinding buffer. Starch gel concentration was 12.5%.

The following enzymes were examined: aspartate aminotransferase (AAT), fluorescent esterase (FE), leucine aminopeptidase (LAP), malate dehydrogenase (MDH), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), shikimate dehydrogenase (SkDH), and triosephosphate isomerase (TPI). AAT, FE, LAP, PGI, and TPI were resolved on a modification of gel and electrode buffer system 8 of Soltis et al. (1983); the gel buffer was composed of 0.033 M tris, 0.005 M citric acid, 0.004 M lithium hydroxide, 0.030 M boric acid, pH 7.6, and the electrode buffer was composed of 0.039 M lithium hydroxide, 0.263 M boric acid, pH 8.0. MDH, PGM, and SkDH were resolved on gel and electrode buffer system 9 of D. Soltis et al. (1983). Staining for all enzymes followed D. Soltis et al. (1983), except LAP, which followed Soltis and Rieseberg (1986).

The genetic control of electrophoretic banding patterns was readily interpreted based on the known subunit structure and subcellular localization of the enzymes (Gottlieb, 1981, 1982). Loci were numbered sequentially, with the most anodally migrating locus designated *1*, the second most anodal locus *2*, and so on. Similarly, allozymes were denoted alphabetically, with the fastest migrating allozyme designated *a*, the second fastest allozyme *b*, and so on.

Results

Morphology.—Table 1 compares *P. kruckebergii*, *P. munitum*, and the putative hybrids for 11 distinguishing morphological features. In many cases, the putative hybrids were intermediate to the parental species, though the hybrid did not exhibit uniform intermediacy. For example, the ratio of pinna length to pinna width, reduction of lower pinnae to triangular segments, and the rotation of pinnae from the plane of the rachis were all closer to the condition of *P. kruckebergii*. In contrast, the rather slight degree of pinna dissection, the frond texture, and the marginal teeth of the pinnae were all more typical of *P. munitum*. The non-costal infralaminar scales are noteworthy in that scales representing both of the parental phenotypes, as well as intermediate conditions, could be found on a single pinna.

Spores are one feature in which hybrid intermediacy was not consistently expressed. *Polystichum munitum* has small, yellowish, translucent spores that average 33 μm in length. Spores of the tetraploid *P. kruckebergii* are much larger, averaging 42 μm in length; they are dark brown in color and are only slightly translucent. Spores of both species are distinctly monolete and relatively uniform in size. In contrast, spores of the hybrid are generally spherical, when not shriveled and malformed. It is noteworthy, however, that many of the spores taken from the hybrid plants were large and well formed. These large, spherical spores

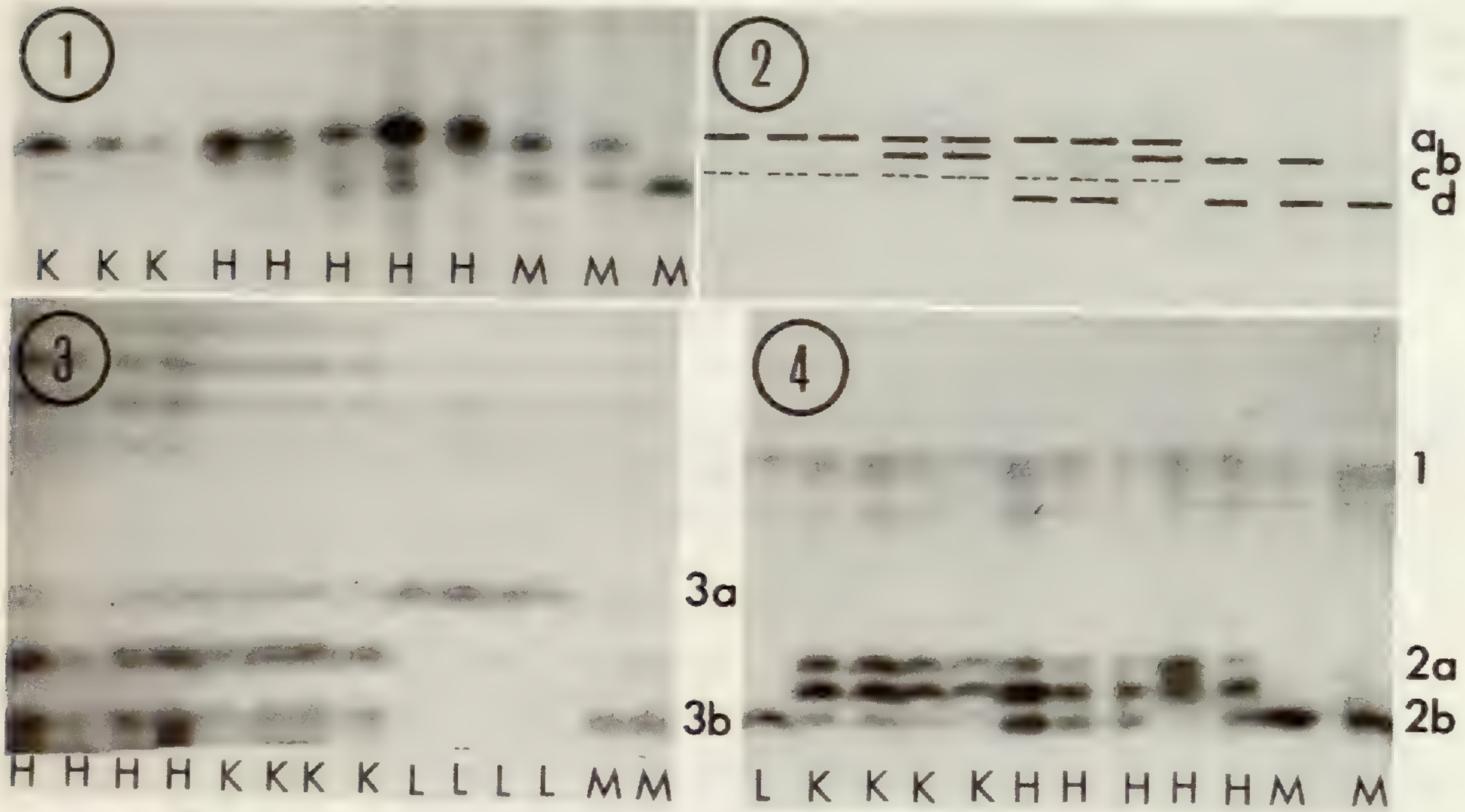
TABLE 1. Morphological Characteristics of *P. kruckebergii*, *P. munitum*, and Their Hybrid.

	P. kruckebergii	hybrid	*P. munitum*
1) Ratio of pinna length to its width at mid-point of pinna	approximately 2:1	approximately 3:1	approximately 6:1
2) Shape of lowest pinnae	triangular with nearly equilateral sides	triangular to ovate-lanceolate	lanceolate
3) Pinna orientation in nature	rotated relative to the axis of the rachis	rotated relative to the axis of the rachis	plane relative to the axis of the rachis
4) Dissection of pinnae	pinnae fully pinnatifid, at least the first 1–3 lobes	pinnae dissected ⅓–⅔ way to the costa	pinna margins toothed, sometimes incised, but not dissected
5) Teeth of the pinna margins	teeth tending to be spreading	teeth tending to be incurved	teeth mostly strongly incurved
6) Frond texture	somewhat soft	firm	firm
7) Indusium margin	more or less entire	erose, with occasional cilia	long ciliate
8) Non-costal infralaminar scales	nearly linear, mostly with few, short basal projections	variable; ranging from short with many basal projections to lanceolate or linear-lanceolate, with few or no basal projections	lanceolate, with an arachnoid base, the basal projections often as long as the body of the scale
9) Spore shape	monolete, uniform	spherical, or shrunken and irregular, often variable in size and outline	monolete, uniform
10) Spore color	dark brown, somewhat translucent	dark brown, opaque	yellowish-brown, translucent
11) Mean exospore length (S.D.)	43 μm (5 μm)	42 μm (8 μm)	33 μm (2 μm)

may be unreduced "mitospores" similar to those described by Morzenti (1962). Morphological characteristics of the putative hybrids and the circumstances under which the hybrids occur clearly suggest that these plants originated by hybridization between *P. kruckebergii* and *P. munitum*.

Electrophoresis.—Eleven loci were interpreted: *Aat*, *Fe-1*, *Lap*, *Mdh-1*, *Pgi-2*, *Pgm-1*, *Pgm-2*, *Skdh*, *Tpi-1*, *Tpi-2*, and *Tpi-3*. The observed enzyme bands migrated anodally for all enzymes.

To document hybridization, electrophoretic investigations of hybridization require genetic markers differentiating the putative parental species. The three possible parental species, *P. munitum*, *P. kruckebergii*, and *P. lonchitis*, possess different genotypes for *Fe-1*, *Lap*, *Pgm-1*, *Pgm-2*, and *Tpi-3* (Figs. 1–3). At *Lap*,



FIGS. 1–4. Starch gels in *Polystichum*. In all figures, numbers and letters in margins designate loci and alleles, respectively. K = *Polystichum kruckebergii*; M = *P. munitum*; L = *P. lonchitis*; H = hybrid. 1. LAP. 2. Interpretive drawing of Fig. 1. 3. TPI. 4. PGI.

all individuals of *P. kruckebergii* possessed the fixed heterozygous genotype *Lap-ac* (Figs. 1, 2). *Polystichum lonchitis* exhibited only allele *Lap-c*, and plants of *P. munitum* displayed *Lap-b*, *Lap-d*, or both of these alleles (Figs. 1, 2). The five putative hybrids possessed one of the following genotypes: *Lap-abc* (three individuals) or *Lap-acd* (two individuals), clearly combining the genotypes of *P. munitum* and *P. kruckebergii* (Figs. 1, 2).

At *Fe-1*, three of the putative hybrids possessed allele *Fe-1b*, the allele found in all *P. kruckebergii* individuals examined. Another putative hybrid possessed the genotype *Fe-1bc*, combining allele *b* of *P. kruckebergii* and allele *c* which was found in all individuals of *P. munitum* from the hybrid site. One putative hybrid did not display FE activity. All individuals of *P. lonchitis* exhibited allele *d*. Data from *Fe-1* therefore provide limited support for the hypothesis that the hybrids are derived from *P. kruckebergii* and *P. munitum*.

Although the putative hybrids possessed identical enzyme bands to those of *P. kruckebergii* at *Pgi-2*, the staining intensities of these bands were clearly different (Fig. 4). All individuals of the tetraploid *P. kruckebergii* exhibited the fixed heterozygous pattern typical of an allotetraploid, with balanced staining. However, dosage effects were observed in the putative hybrids. All of the putative hybrids displayed unbalanced heterozygosity at *Pgi-2* (Fig. 4). Four individuals possessed extra doses of allele *b*, the allele typical of *P. munitum* and *P. lonchitis*, and one individual had an additional dose of allele *a*, an allele present in the fixed heterozygous pattern of *P. kruckebergii* and observed in other populations of *P. munitum* (P. Soltis & D. Soltis, 1987). Unbalanced staining would be expected in a triploid hybrid between a diploid and an allotetraploid that share alleles.

The other loci examined did not provide information useful in determining

the parentage of the hybrids. *Polystichum kruckebergii* can be distinguished from *P. munitum* and *P. lonchitis* at *Tpi-1* and *Tpi-2*, but the latter two species cannot be differentiated (Fig. 3). The tetraploid *P. kruckebergii* exhibited fixed heterozygosity at *Tpi-3* (Fig. 3). In addition, a five-banded pattern was observed in the more anodal zone of activity for TPI (Fig. 3). However, it is unknown whether this represents fixed heterozygosity at *Tpi-1* or *Tpi-2* or both of these loci. The putative hybrid could not be distinguished from *P. kruckebergii* at any of the TPI loci (Fig. 3).

The loci *Aat*, *Mdh-1*, and *Skdh* were monomorphic for all plants examined. Although the three possible progenitors were differentiated at *Pgm-1* and *Pgm-2*, the banding patterns were not clearly resolved in the putative hybrids.

Discussion

The morphological and allozymic data presented herein confirm the occurrence of hybridization between *Polystichum munitum* and *P. kruckebergii*. The putative hybrids are morphologically intermediate between the proposed parental species for several characters. Furthermore, the hybrids clearly combine the alleles of *P. munitum* and *P. kruckebergii* at *Lap*. The data obtained for all other loci examined are also consistent with this hypothesis of hybridization. The data for *Lap* and *Fe-1* rule out the possibility that *P. lonchitis* is one of the parental species.

In the five hybrid individuals examined we detected three different genotypes across all loci. This indicates that hybridization between different *P. munitum* and *P. kruckebergii* individuals occurred at least three times in this mixed population; the several hybrid individuals were not the result of vegetative reproduction following a single hybridization event.

Because the tetraploid *P. kruckebergii* is thought to have *P. lemmonii* and *P. lonchitis* as its diploid progenitors (W. Wagner, 1973; D. Wagner, 1979), the genomic composition of the hybrids presumably comprises three distinct genomes: *P. munitum*, *P. lonchitis*, and *P. lemmonii*. This combination could also result from a hybrid between *P. lonchitis* and *P. scopulinum*, provided that at least some populations of *P. scopulinum* have the parentage *P. lemmonii* × *munitum* s. s., as proposed by W. Wagner (1973). More recently, however, D. Wagner (1979) suggested that the once-pinnate diploid progenitor of *P. scopulinum* was *P. imbricans* rather than *P. munitum*. Further allozymic investigations should provide additional information regarding evolutionary relationships in this species complex.

The detection of yet another interspecific hybrid in *Polystichum* is not surprising, particularly given the widespread occurrence of hybridization within the genus (Knobloch, 1976; Tryon & Tryon, 1982; Mickel in Barrington, 1985; W. Wagner in Barrington, 1985). It is noteworthy that five of the seven interspecific *Polystichum* hybrids previously reported from western North America involve *P. munitum* as a parental species. This may be due to the more widespread distribution of this species, relative to other western North American *Polystichum* species. However, the frequency with which *P. munitum* hybridizes with other

species may also reflect the breeding system of this species. *Polystichum munitum* is almost completely outcrossing; intragametophytic selfing estimates in populations of *P. munitum* ranged from 0 to 3% (P. Soltis & D. Soltis, 1987). This outcrossing breeding system provides the potential for interspecific hybridization whenever *P. munitum* occurs in the same locality as other *Polystichum* species. Other *Polystichum* species are also outcrossing. For example, in *P. imbricans* intragametophytic selfing estimates ranged from 0 to 17% (D. Soltis and P. Soltis, 1987). Data regarding the mating systems of *P. kruckebergii* and other *Polystichum* species are not yet available; however, the frequency of hybridization in this genus suggests that high outcrossing rates may be typical of other species of *Polystichum*.

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LITERATURE CITED

BARRINGTON, D. S. 1985. The present evolutionary and taxonomic status of the fern genus *Polystichum*: The 1984 Botanical Society of America Pteridophyte Section Symposium. Amer. Fern J. 75:22–28.

———. 1986. The morphology and cytology of *Polystichum* × *potteri hybr. nov.* (= *P. acrostichoides* × *P. braunii*). Rhodora 88:297–313.

CALLAN, A. D. 1972. The cytotaxonomic study of a triploid *Polystichum munitum* × *californicum* hybrid from Douglas County, Oregon, with some observations on the varieties of *Polystichum munitum*. M.S. Thesis. Southern Oregon College, Ashland, Oregon.

COPELAND, E. B. 1947. *Genera filicum*. Waltham, Massachusetts: Chronica Botanica.

DAIGOBO, S. 1974. Chromosome numbers of the fern genus *Polystichum*. J. Jap. Bot. 49:371–378.

GOTTLIEB, L. D. 1981. Electrophoretic evidence and plant populations. Prog. Phytochem. 7:1–45.

———. 1982. Conservation and duplication of isozymes in plants. Science 216:373–380.

KNOBLOCH, I. W. 1976. Pteridophyte hybrids. Publ. Mus. Michigan State Univ. Biol. Ser. 5:277–352.

MANTON, I. 1950. *Problems of cytology and evolution in the Pteridophyta*. Cambridge: Cambridge University Press.

MORZENTI, V. M. 1962. A first report on pseudomeiotic sporogenesis, a type of spore reproduction by which "sterile" ferns produce gametophytes. Amer. Fern J. 52:69–78.

NAKAIKE, T. 1973. Studies in the fern genus *Polystichum*. I. Observations on the section *Metapolystichum* at Gobo-sawa, Pref. Chiba. Bull. Nat. Sci. Mus. Tokyo 16:437–457.

SLEEP, A. and T. REICHSTEIN. 1967. Der Farnbastard *Polystichum* × *meyeri hybr. nov.* = *Polystichum braunii* (Spenner) Fée × *P. lonchitis* (L.) Roth und seine Cytologie. Bauhinia 3:299–314.

SOLTIS, D. E., C. H. HAUFLER, D. C. DARROW, and G. J. GASTONY. 1983. Starch gel electrophoresis of ferns: A compilation of grinding buffers, gel and electrode buffers, and staining schedules. Amer. Fern J. 73:9–27.

——— and L. H. RIESEBERG. 1986. Autopolyploidy in *Tolmiea menziesii*: Genetic insights from enzyme electrophoresis. Amer. J. Bot. 73:310–318.

——— and P. S. SOLTIS. 1987. Polyploidy and breeding systems of homosporous Pteridophyta: A re-evaluation. Amer. Naturalist 130:219–232.

SOLTIS, P. S. and D. E. SOLTIS. 1987. Population structure and estimates of gene flow in the homosporous fern *Polystichum munitum*. Evolution 41:620–629.

THOMPSON, R. H. and R. L. COFFIN. 1940. A natural hybrid between *Polystichum braunii* (Spenner) Fée and *P. acrostichoides* (Michx.) Schott. Amer. Fern J. 30:81–88.

TRYON, R. M. and A. F. TRYON. 1982. *Ferns and allied plants with special reference to tropical America.* New York: Springer-Verlag.

WAGNER, D. H. 1979. Systematics of *Polystichum* in western North America North of Mexico. Pteridologia 1:1–64.

WAGNER, W. H., Jr. 1968. Hybridization, taxonomy, and evolution. Pp. 113–118 in *Modern methods in plant taxonomy,* ed. V. H. Heywood. London: Academic Press.

———. 1973. Reticulation of holly ferns (*Polystichum*) in the western United States and adjacent Canada. Amer. Fern J. 63:99–115.

——— and D. J. HAGENAH. 1954. A natural hybrid of *Polystichum lonchitis* and *P. acrostichoides* from the Bruce Peninsula. Rhodora 56:1–6.

REVIEW

"*Iconographia palynologica pteridophytorum Italiae,*" by E. Ferrarini, F. Ciampolini, R. E. G. Pichi Sermolli, and D. Marchetti. Webbia 40:1–202. 1968.

This collaborative work, in Italian, by three biologists at the University of Siena and R. E. G. Pichi Sermolli at the University of Perugia, has resulted in an impressive series of scanning electron micrographs of spores of the 65 species of Italian Pteridophyta. More than 500 SEM's, assembled in 71 plates, include 3–8 figures and surface details for each taxon. The conservative nature of spores is evident in the similar details of surface and elators of the nine species of *Equisetum.* Similarities of surface contours in many genera with monolete spores suggest there may be broad, general alliances between these genera.

An extensive glossary, illustrated by fine drawings, includes terms as nexine and sexine, not applicable to spores. The binary key to genera, based on spore morphology is not easily used. Differences of a few microns in the headings leading to *Phyllitis* and *Asplenium* or to species of *Polypodium* are difficult choices. The heading "Spore senze perina" leading to *Polypodium* unfortunately is an inaccuracy that undoubtedly persists from light microscope observations in which the perine was not evident. Scanning and transmission microscope work on spores show, with few exceptions, that spores of all Filicineae have perine, or perispore.

In addition to descriptions of the spores, the text consists of comments on nomenclature and the cytology of the species. In light of the emphasis on cytology it is disappointing to find the SEM magnifications are inconsistent. Differences in size of spores of *Asplenium ruta-muraria,* shown at × 1080 for the autotetraploid subsp. *ruta-muraria,* and at × 750 for the diploid subsp. *dolomitica,* cannot be readily visualized.

This atlas of spores will be particularly valued as a reference for comparison of surface morphology of these 65 species with that of spores from other regions.

The fine details depicted in SEM spore studies such as this require special attention to reproduction of the micrographs for publication. This unfortunately has contributed to the cost of this volume, which at 130,000 lira, is somewhat more than one hundred dollars.—ALICE F. TRYON, Harvard University Herbaria, Cambridge, MA 02138.

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Growth Patterns of Gemmlings of *Lycopodium lucidulum*

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Knowledge of branching patterns in *Lycopodium* is often based on herbarium specimens of mature plants or parts of plants. Comparative studies of the architecture and chronological events have received little attention. Most information concerns the mode of dichotomy or stelar structure in plant parts of different age (Ogura, 1972). Primack (1973) compared shoot growth patterns in five species of *Lycopodium*.

Investigations of the ontogeny of young plants and their changes as they reach maturity are limited by the difficulties in collecting gametophytes and young sporophytes of different age. There are few references to the growth pattern of vegetatively propagated plantlets and their chronological development (Bruchmann, 1898; Troll, 1937, for *L. selago*).

The present study of *Lycopodium lucidulum* Michaux is concerned with the method of elaboration of a mature plant from a single gemma. As *L. lucidulum* grows and branches very slowly in time, plants of different age had to be compared to analyze ontogenetic changes.

MATERIALS AND METHODS

Lycopodium lucidulum populations were studied in the understory of mixed hardwoods at Harvard Forest, Petersham, Massachusetts. These occur in old forests dominated by white pine and red maple and particularly in wet undisturbed forests close to small streams.

Measurements and drawings of old individual plants were done in the field; whole smaller clumps were removed and studied in the laboratory. To analyze the growth in length within a definite period, eight erect axes were marked with ribbons at a measured distance from the apex. From this fixed point the additional growth of the apices was noted at weekly intervals over a period of 5 months (19 April to 13 September, 1986) (Fig. 1). An additional estimate of the yearly growth was provided by a single axis (marked in 1978 by K. Esseichick) which showed a similar average to that of the 8 more recently marked axes.

RESULTS

Deterministic shoot dynamics.—*Lycopodium lucidulum* has erect axes that duplicate themselves through equal dichotomy (isotomy) of the apices. Mature shoots of *L. lucidulum* lack definite strobili but have alternating vegetative and fertile zones along the stem (Fig. 2). Microphylls or vegetative leaves are longer

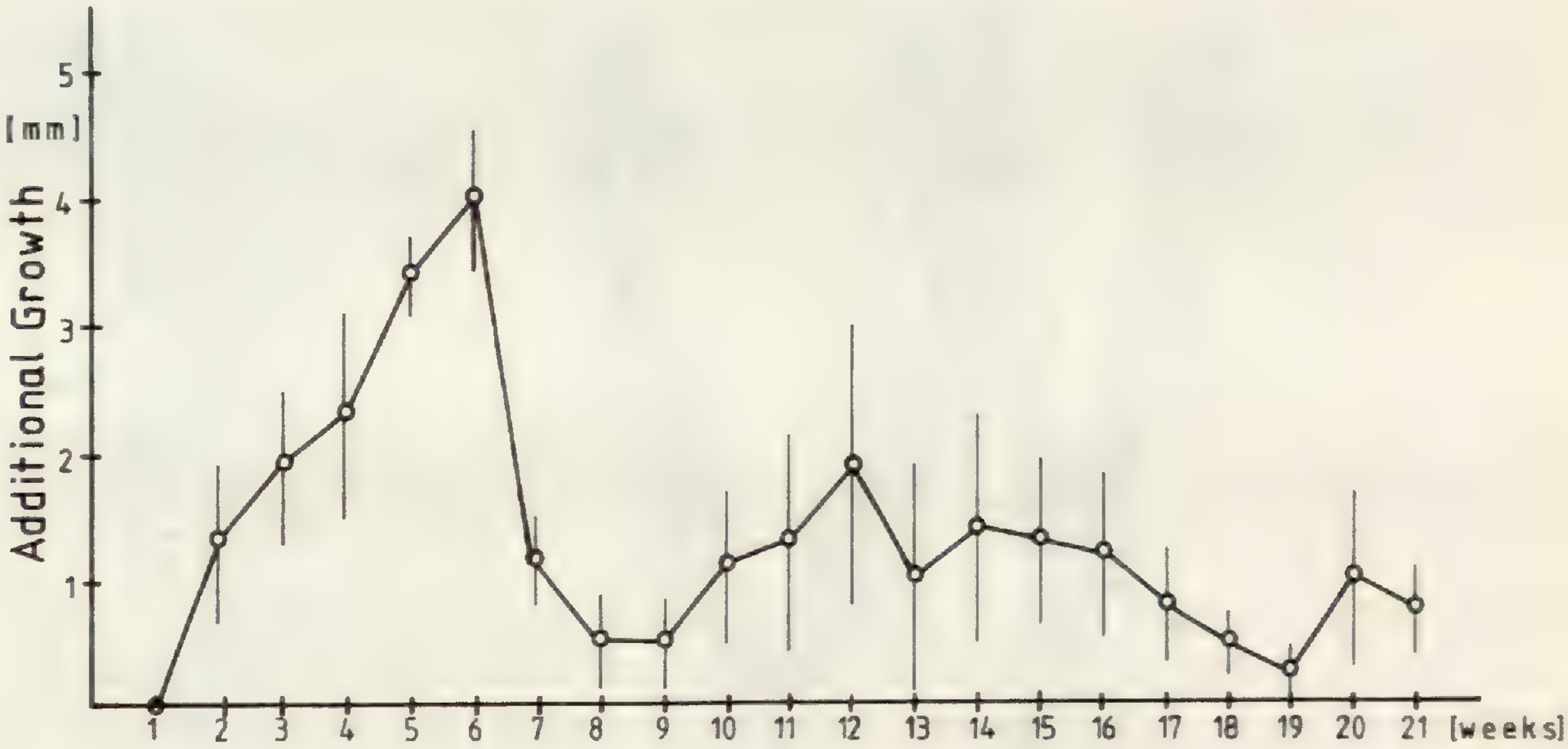


FIG. 1. Shoot extension in *Lycopodium lucidulum* (additional growth in length per week) during one growth period (19 Apr 1986 to 31 Sept 1986). Bars represent standard deviation (n = 8).

(12 mm) and wider (2 mm) than the sporophylls (fertile leaves), which are 5 mm long and less than 1 mm wide. There is an abrupt transition between these different types with only 1–2 whorls of an intermediate size.

The shoot complexes have a certain "individual" size because of simultaneous additional growth at the distal green end and rotting at the rhizomatous creeping end (Table 1). Erect distal axes retain a uniform height because older parts recline to a prostrate position with yellowing microphylls indicating loss of chlorophyll ("transition zone") (Table 1).

The lower portion of older, now rhizomatous axes becomes covered by accumulated leaf litter within which root develpment is pronounced. Rhizome length may be arbitrarily measured from the point of the youngest visible root that is just penetrating the stem cortex to the oldest persistent part of the axis.

Roots are initiated endogenously. Some root primordia can be found near the apex, associated either with two branches of a dichotomy or within the zone of the main yearly growth increment, indicated externally by larger vegetative microphylls. Root initials are much delayed in their further development. Additional, possibly adventitious, root primordia can be found in older parts of the shoot. The region where root extension is most pronounced seems to be the transition zone. Here the root meristems develop and grow about 1–2 cm inside the cortex in proximal direction. They break through the cortex at irregular distances from their origin and fix the now horizontal part of the axis to the ground.

Field observations, growth measurements, and dissection of winter buds suggest that the small sporophylls are preformed late in the vegetative period of the previous growing season but remain enclosed in the apical bud during the winter. Dissection of a bud in early spring shows the sporophylls bearing immature sporangia. The large vegetative microphylls appear later during the main growth period in April to June, i.e., they are newly formed.

2

3

FIGS. 2, 3. *Lycopodium lucidulum*. 2. Mature shoot (fragment) with alternating zones of sporophylls and larger microphylls. Gemmaphores of the recent growth period with gemmae. 3. Gemmling with gemma still attached.

In this period of vegetative growth, the plant also produces gemmae. Axes that are to branch also will undergo isotomy at this time. The age of a shoot can be estimated from fluctuation in leaf size since a single vegetative and fertile zone develops each year. Growth measurement of some shoots during the 5 month monitoring period confirmed the seasonal cycle (Fig. 1). The decrease of the growth rate in June is probably related to the unusually high rainfall and low

TABLE 1. Average Growth Measurements of a Mature "Individual" of *Lycopodium lucidulum*; n = 15.

	Mean	Range
Total length of "individual"	31.9 ± 6.5	21–47 cm
Height of erect green axis	12.8 ± 2.5	9–19 cm
Length of transition zone	4.6 ± 1.4	2–7 cm
Length of rhizome	14.5 ± 7.2	4–33 cm
Age of "individual"	13.4 ± 2.8	10–20 years
Additional growth	2.4 ± 1.7	2.1–2.7 cm/year
Number of dichotomies	3.1 ± 1.1	2–5
Time interval between two dichotomies	4.3 ± 1.7	2–7 years

temperature during this period. Case (1943) described a similar zonation pattern for *L. selago*, although this species shows a different development in time. Sporangia are initiated in early summer and need about two years for ripening; gemmae are laid down in mid-summer and are shed in fall of the following year.

Equal branching of the apical meristem occurs only in the green, erect shoots. The number of terminal axes (x) follows the simple relationship

$$x = 2^n$$

where n is the number of previous dichotomies. This regular pattern can be found in many gemmlings (i.e., young plants derived from gemmae; Stevenson, 1976). In older plants the regular system is often disturbed by damage and consequent loss of one or more shoots. No deterministic mechanism for the development of additional branches as a response to damage was observed, so that a lost branch is irreplaceable. The total number of branches (x) on the plant therefore diminishes from the ideal number according to the relation

$$x = 2^n - 2^{n-a}$$

(for an injury at the a-th dichotomy) or

$$x = 2^n - 2^{n-a} - 2^{n-b} \ldots$$

(for an injury at the a-th and b-th and . . . dichotomy). There is no evident change in growth form, rate of extension, or branching frequency of one axis of a dichotomy, compared to undamaged shoot pairs, if the corresponding one is damaged. Very occasionally lateral gemmae that fail to become detached can replace a lost main axis, but this is not a deterministic feature of growth.

Gemmae development.—No plants were observed developing from gametophytes. The following information therefore relates only to plants developed from gemmae.

Gemmae are produced on older shoots by structures ("gemmaphores") that have the position of a microphyll but show all features of a shoot (Stevenson, 1976). Typically, the gemmaphore initiates 3 pairs of microphylls that remain on the old stem after gemma separation. The distal part of this gemmaphore develops another 3 pairs of microphylls, one pair of them large and fleshy. This fleshy pair forms a heart-shaped structure (the gemma sensu stricto) that separates from the

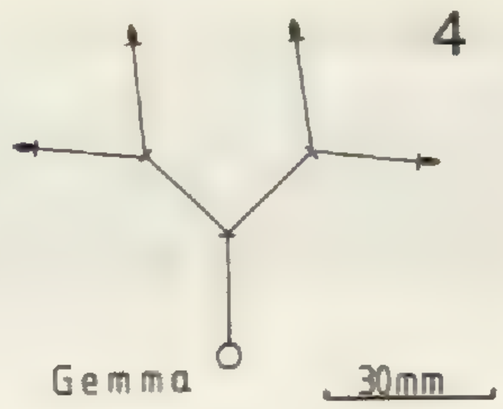
gemmaphore by means of an abscission layer. A root primordium develops on the proximal end of the gemma before abscission occurs.

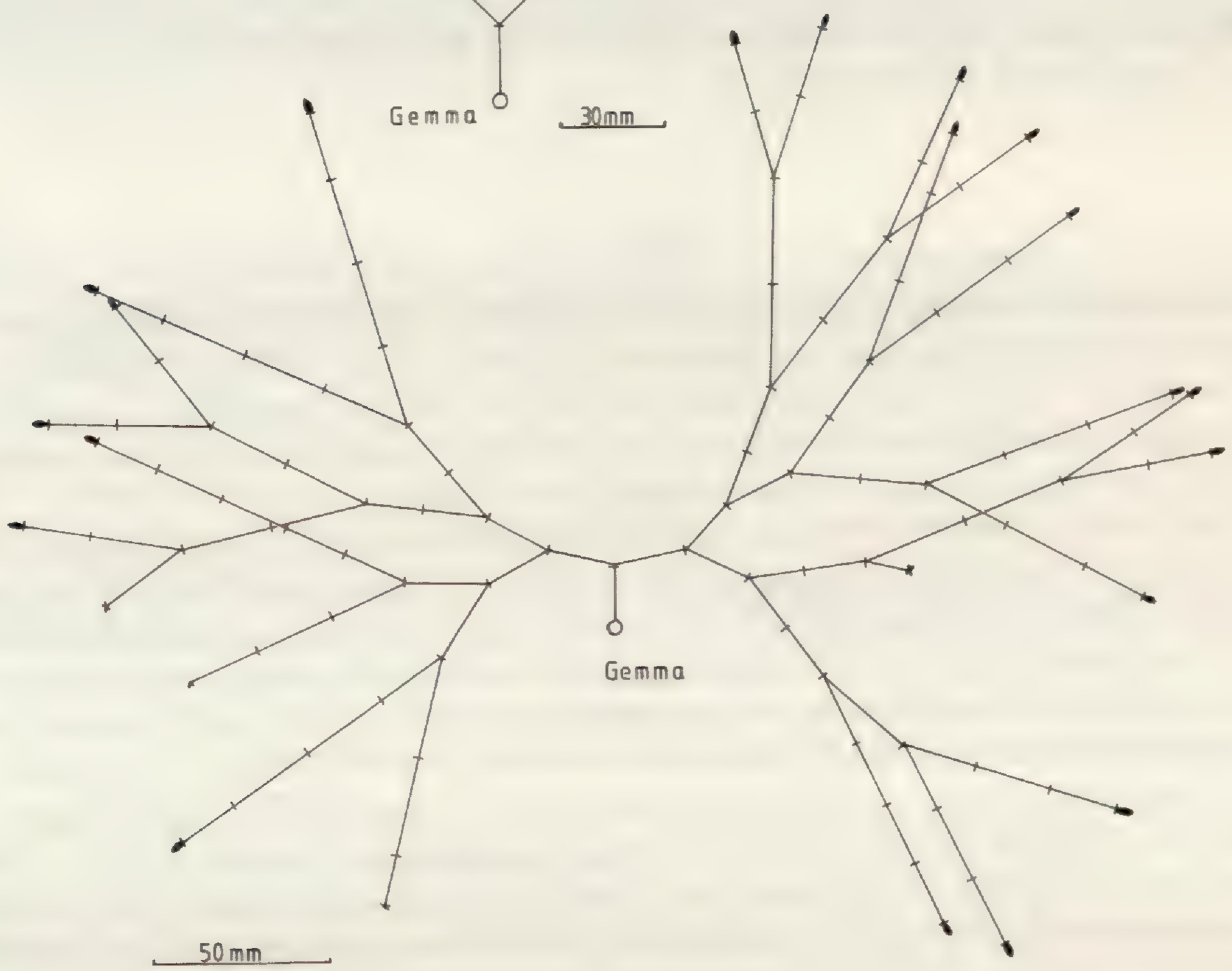
Gemmae are shed in fall and become buried with leaf litter. In the following spring the gemmae develop an axis and microphylls that differ in shape from those of the adult plant (Fig. 3). The length of these first axes depends mostly on the thickness of the covering litter. The covered parts bear few scalelike microphylls. On average the exposed axis of the gemmling in the first season reaches a length of 1.5–3.0 cm with green leaflike structures, which are rounder and about half the size of the adult microphylls (5 × 3 mm). They are arranged in an increasing phyllotactic spiral. Often there are one or two endogenous roots in addition to the first developed gemma root. Usually the two fleshy microphylls become lignified and persistent so that they can be recognized on plants up to 18 years old. This allows the reconstruction of the development and branching pattern of the plant from its first dichotomy.

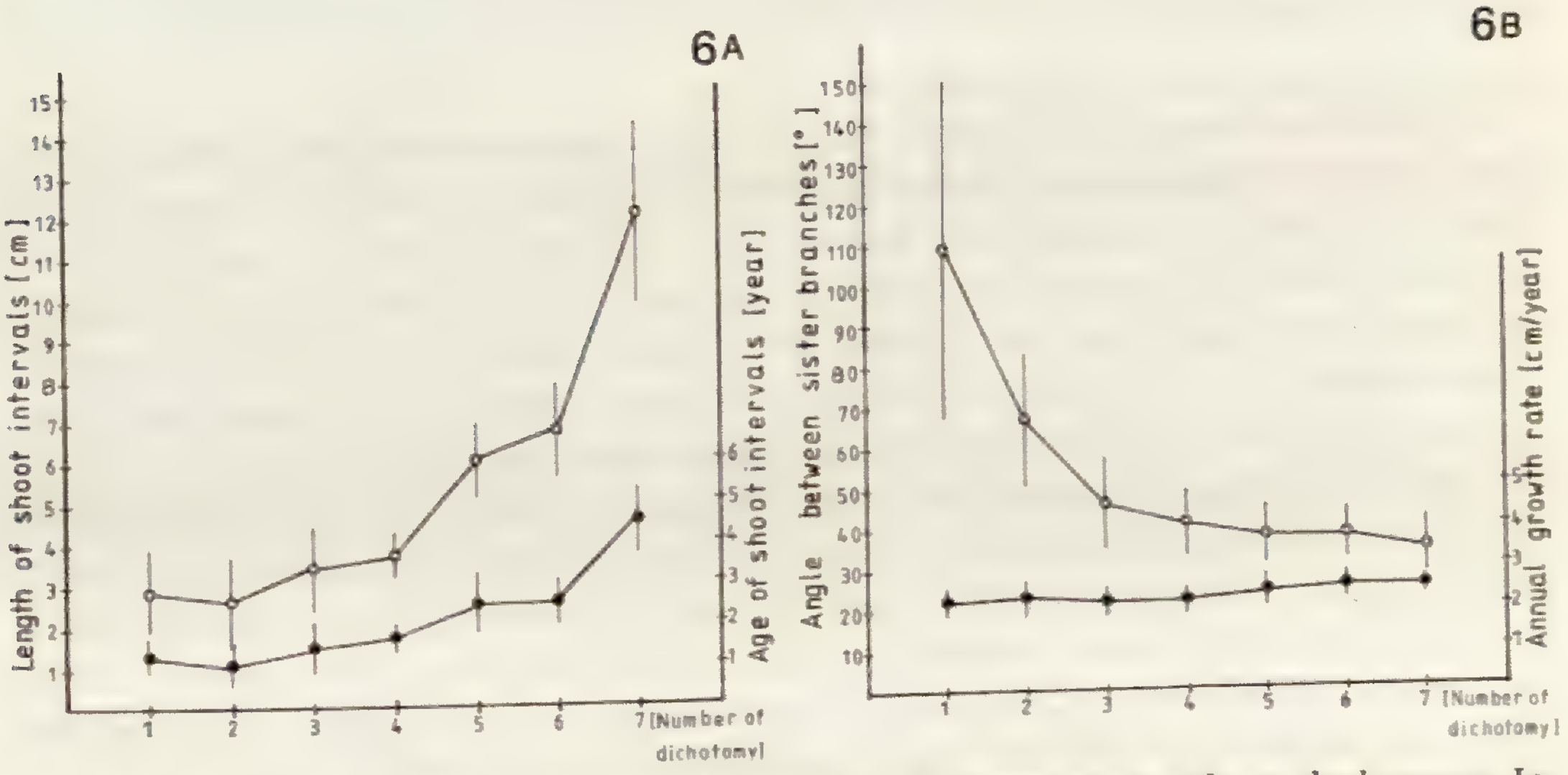
The gemmling undergoes its first dichotomy at the beginning of the second year (Fig. 4). Subsequent dichotomies occur either in the next vegetative period or in later years. Usually the two daughter branches of a dichotomy show the same branching pattern, so that young plants with few branches have a very symmetrical shape (Fig. 5). In comparison with the adult stages there is a measurable tendency in older plants to prolong shoot growth and reduce branching frequency, expressed in the increasing distance between two successive dichotomies (Fig. 6A). The delay of branching can be recognized by the seasonal change in leaf size, which is first shown by the plant in its second or third year. Although no sporangia are produced on plants of this age, one can distinguish larger from smaller microphylls, the latter equivalent in shape and size to sporophylls. Annual growth periodicity is the same as in the adult plant; little variation results from different climatic or nutritional circumstances (Fig. 6B).

The internal angle between two daughter branches of one dichotomy decreases from a range of 90°–180° in the first dichotomy to 20°–30° in the dichotomies of the mature shoot (Fig. 6B). The planes of the first and second dichotomy, independent of the angle between the daughter shoots, regularly are arranged in an interplanar angle of 90°, described as "cruciate" by Troll (1937) for *Lycopodium selago*. Subsequent inclinate orientation of dichotomy planes (Øllgaard, 1979) shows interplanar angles with less than 30°, which means that all descendants of each branch resulting from the first dichotomy are arranged with their apices in a half circle. This variation of the branching angles, together with the increasing shoot growth increments results in the arrangement of the erect shoots in "growth-rings" or "fairy-rings" (Fig. 5). The largest diameter of a plant observed with an attached basal gemma was about 50–60 cm. In older stages, the original orientation towards a center of origin is less easily recognizable.

Gemmlings bear the first sporangia at an age of 6–7 years. Daughter gemmae appear about 2 years later. This change to fertility seems independent of the frequency of previous dichotomies. With increasing age and diameter the oldest parts of the plant decay and the distal shoots become separated. The persistent fragments, consisting usually of 2–8 connected shoots resulting from the most recent 1–3 dichotomies, have several functional apical meristems at their distal







FIGS. 4–6. Branching pattern in *Lycopodium lucidulum*. 4. Young plant with attached gemma. Intervals represent growth of one year. Angle between shoots and length of intervals as in nature. 5. Nine year old plant. X-marked shoots are damaged. Angle between shoots and length of intervals as in nature. 6A. Length of shoot intervals between dichotomies of different rank (open circles). Corresponding age of shoot intervals between dichotomies (closed circles). Bars represent standard deviation (n = 10). 6B. Annual growth rate of shoot intervals of different age and length (closed circles). Angle between the sister branches of dichotomies of increasing grade (open circles). Bars represent standard deviation (n = 10).

ends. In this way new "individuals" (ramets) are recognized (Fig. 2). The branching pattern of each single fragment shows no specific relation to other fragments and is the same as described for the mature plant in Table 1. The variation observed is large. The unusual synchrony of dichotomies therefore occurs only in "young" stages of development.

Discussion

Branching, by multiplying meristems, is used to define the growth units out of which a modular organism is composed (Harper & Bell, 1979). *Lycopodium lucidulum*, as a clonal plant, repeats a simple pattern: prolongation of each axis for a certain distance, and division of the apical meristem into two equal portions, which each grow the same length before dichotomizing again.

The plant (population of fragments) therefore shows an intrinsic exponential growth within a constant time unit. However, in contrast to the continuous population growth described for other plants (Harper & White, 1974), *L. lucidulum* produces gemmae as an additional vegetative method of multiplying. These follow different rules of growth per time unit. The analysis of a plant growing from a gemma shows a controlled change of the modular units, which is expressed in the time interval between two dichotomies. As it ages, the gemmling shows at least two different growth models. It might therefore be possible to find a third developmental pattern in plants developed from gametophytes. Although some similarities exist in pattern of phyllotaxis and microphyll shape (Bruce & Beitel, 1979; Bruchmann, 1899, for *L. selago*) between the first axes of both sexually and asexually initiated shoots, there is no reference to the further development of young sporophytes in the literature.

The organization of *L. lucidulum* can be described as a "creeping clump" (Bell, 1984), but the production of gemmae allows the plant to spread out much faster than by dichotomy. In addition, the gemmae can be interpreted as functional (although detached) reserve meristems. Except for the dichotomy of the apical meristem the plants have no further method to regenerate shoots. Adventive regeneration from old shoots is reported for some members of the section *Urostachya* (Øllgaard, 1979), but without morphological details.

A growth-system different from the "creeping clump" can be found in the "runners" of the *Lepidotis* and *Lycopodium* sensu stricto groups (Wilce, 1972). These plants are remarkable for their unequal dichotomy (anisotomy) in which the minor axis can remain dormant as a reserve meristem. These reserve meristems allow them either to replace damaged shoots or to proliferate under optimal growth conditions, reiterating the growth pattern of the mother axis.

It seems that the growth pattern involving runners is environmentally much more flexible than the rather fixed *L. lucidulum* system. Because of its isotomy the architecture of *L. lucidulum* is restricted in its ability to repair damage, but compensates for this disadvantage by the development of gemmae. This could be interpreted as a derived pattern imposed on an ancestral determinism.

ACKNOWLEDGMENTS

This study was made possible by a scholarship of the DAAD to the author at Harvard Forest, Petersham, Massachusetts. I thank Dr. P. B. Tomlinson for providing facilities and also for suggesting this study. I much appreciate his patience, help, and encouragement during the course of this work and during my stay at Harvard Forest.

LITERATURE CITED

BELL, A. D. 1984. Dynamic morphology: a contribution to plant population ecology. Pp. 48–65 in *Perspectives on plant population ecology*, ed. R. Dirzo and J. Sarukhan. Sunderland, Mass.: Sinauer.

BRUCE, J. G. and J. M. BEITEL. 1979. A community of *Lycopodium* gametophytes in Michigan. Amer. Fern J. 69:33–41.

BRUCHMANN, H. 1898. Über die Prothallien und die Keimpflanzen mehrerer europäischer Lycopodien. Gotha.

CASE, I. M. 1943. Periodicity in the development of fertile and sterile zones in *Lycopodium selago*. New Phytol. 42:93–97.

HARPER, J. L. AND A. D. BELL. 1979. The population dynamics of growth form in organisms with modular construction. Pp. 29–52 in *Population dynamics*, ed. R. M. Anderson et al. The 20th Symposium of The British Ecological Society, London.

——— and J. WHITE. 1974. The demography of plants. Annual Rev. Ecol. Syst. 5:419–463.

OGURA, A. Y. 1972. *Comparative anatomy of vegetative organs of the pteridophytes*. Berlin: Gebrüder Borntraeger.

ØLLGAARD, B. 1979. Studies in Lycopodiaceae II: The branching patterns and infrageneric groups of *Lycopodium* s.l. Amer. Fern J. 69:49–61.

PRIMACK, R. B. 1973. Growth patterns of five species of *Lycopodium*. Amer. Fern J. 63:3–7.

STEVENSON, D. W. 1976. Observations on the phyllotaxis, stelar morphology, the shoot apex and gemmae of *Lycopodium lucidulum* Michaux (Lycopodiaceae). J. Linn. Soc., Bot. 72:80–100.

TROLL, W. 1937. *Vergleichende Morphologie der höheren Pflanzen*. Bd. 1, Teil 1:465–483. Berlin: Gebrüder Borntraeger.

WILCE, J. H. 1972. Lycopod spores I. General spore patterns and the generic segregates of *Lycopodium*. Amer. Fern J. 62:65–79.

American Fern Journal 77(2):58–63 (1987)

The Expanded Adaxial Epidermis of *Equisetum* Rhizome Sheath Teeth

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Plants of *Equisetum* have an extensive rhizome system that produces nodal buds that grow into either aerial stems or branches of the rhizome. Certain species also have tuber buds. Both the aerial stems and the rhizomes of *Equisetum* have nodal sheaths bearing a crown of teeth. The sheath is interpreted as a whorl of fused leaves, with the teeth representing the free tips of the individual leaves. The buds consist of a series of superposed sheaths that overarch the shoot apex. Subsequent intercalary meristematic activity at the base of each nodal sheath separates the nodal sheaths and produces the internodes.

The sheath teeth of the subterranean buds have a distinctive adaxial epidermis, a feature rarely noted in the literature. Francini (1942) compared rhizome and aerial buds of *E. ramosissimum*, and described trichomes developing from the inner epidermis of the rhizome sheath teeth and growing together to help the teeth form a cap protecting the apex. She also described mucilage production from the abaxial epidermis of the outer sheaths and pointed out how only one internode at a time elongates in the rhizome. Sachs (1882, p. 401) included a figure of a longitudinal section through an underground bud of *Equisetum arvense* showing an elaboration of the adaxial surface of the sheath teeth, but he did not describe this feature. Sadebeck (1902, p. 532) copied Sachs' figure, but did not mention the structure of the adaxial surface of the teeth. The purpose of this study is to describe more completely this little noted anatomical feature of *Equisetum*, and to speculate on its function.

MATERIALS AND METHODS

Rhizomes of *Equisetum hyemale* L., *E. arvense* L., and *E. telmateia* Ehrh. subsp. *braunii* (Milde) Hauke were excavated, washed, and their buds removed. Potted plants of *E.* ×*schaffneri* Milde, *E. scirpoides* Michx, and *E. diffusum* Don were depotted and rhizome terminal buds removed. The buds were killed and fixed in FAA for 24 hours and then stored in 70% EtOH. Sources of material are given on Table 1.

The outermost sheath was dissected from the bud. The clean bud was dehydrated in a tertiary butyl alcohol series, embedded in Paraplast (56–57°C), sectioned on a rotary microtome at 15 μm (longitudinal sections) or 20 μm (transverse sections), stained with safranin-fast green or safranin-toluidine blue (Berlyn & Miksche, 1976), and mounted in diaphane. Photos were taken on Kodak Plus-X film with a Nikon Microflex UFX camera mounted on a Zeiss microscope.

Buds used for scanning electron microscopy (SEM) were dehydrated in an ethanol series that included two changes of 100% ethanol and critical point dried

TABLE 1. Sources of Material of *Equisetum* Rhizome Buds.

Species	Locality	Voucher[1]
E. arvense	Rhode Island, Galilee	*Hauke 516*
E. arvense	Rhode Island, Kingston	*Hauke 514*
E. diffusum	Greenhouse, Univ. Rhode Island (originally from near Simla, India)	*Hauke s.n.*
E. hyemale var. *affine*	Rhode Island, Galilee	*Hauke 515*
E. ×schaffneri	Greenhouse, Univ. Rhode Island (originally from near San Jose, Costa Rica)	*Hauke 205*
E. scirpoides	Greenhouse, Univ. Rhode Island (originally from near Rutland, Vermont)	*Hauke 490*
E. telmateia subsp. *braunii*	California, Oakland, Claremont Canyon	*Hauke C1*

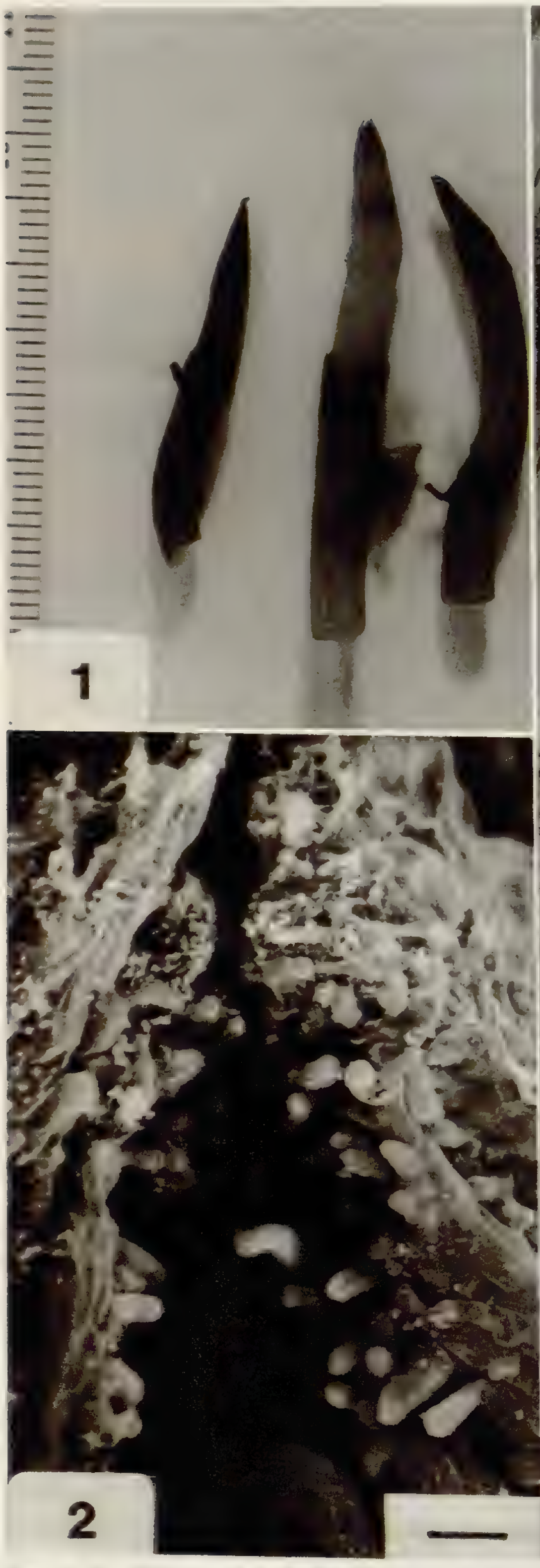
[1] All in KIRI.

using CO_2 substitution and a Tousimis Samdri-PVT-3B critical point drier. They then were mounted on aluminum stubs with double-sided tape, coated with gold-palladium in a Hummer II coater, and observed with a Cambridge S4 scanning electron microscope.

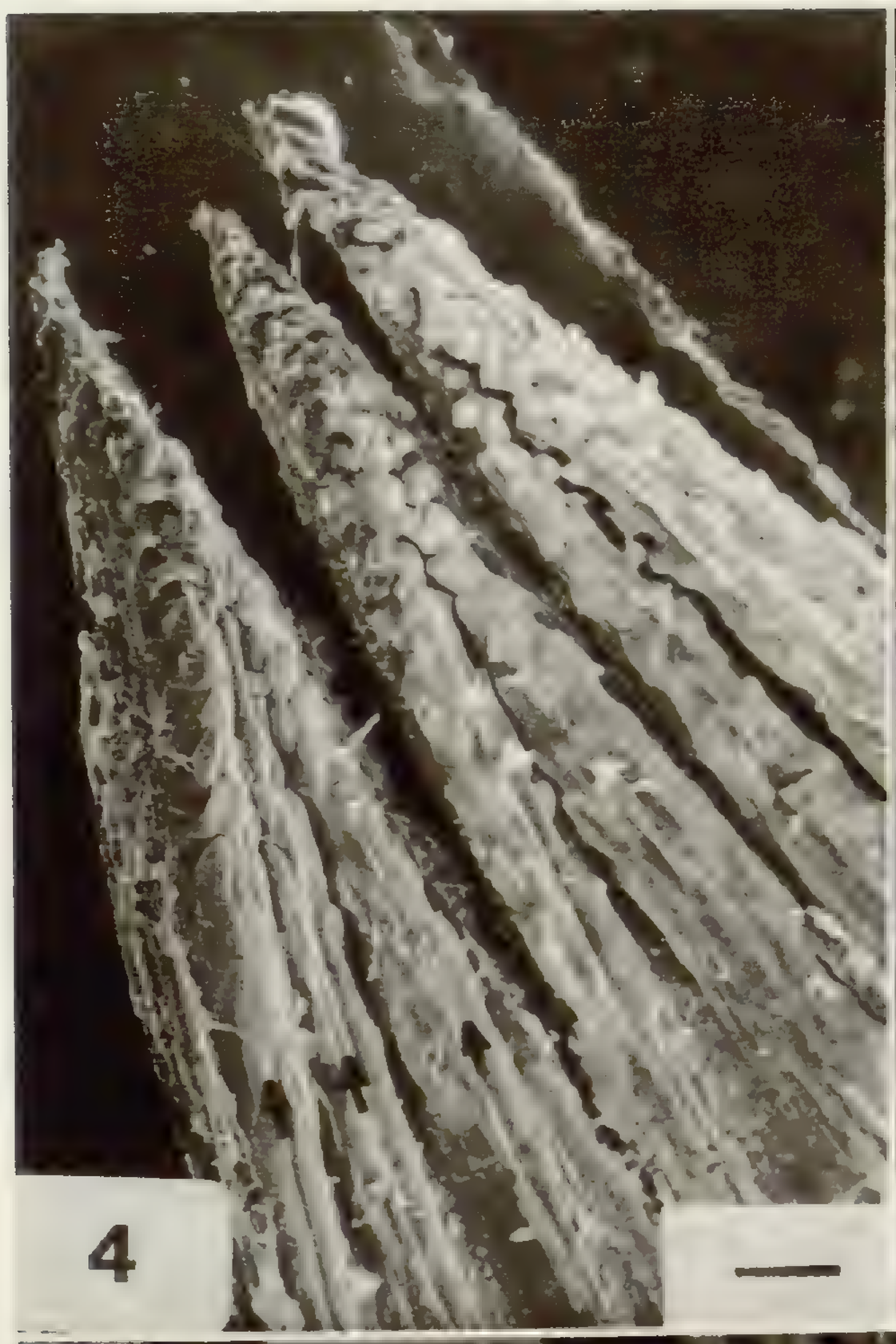
RESULTS

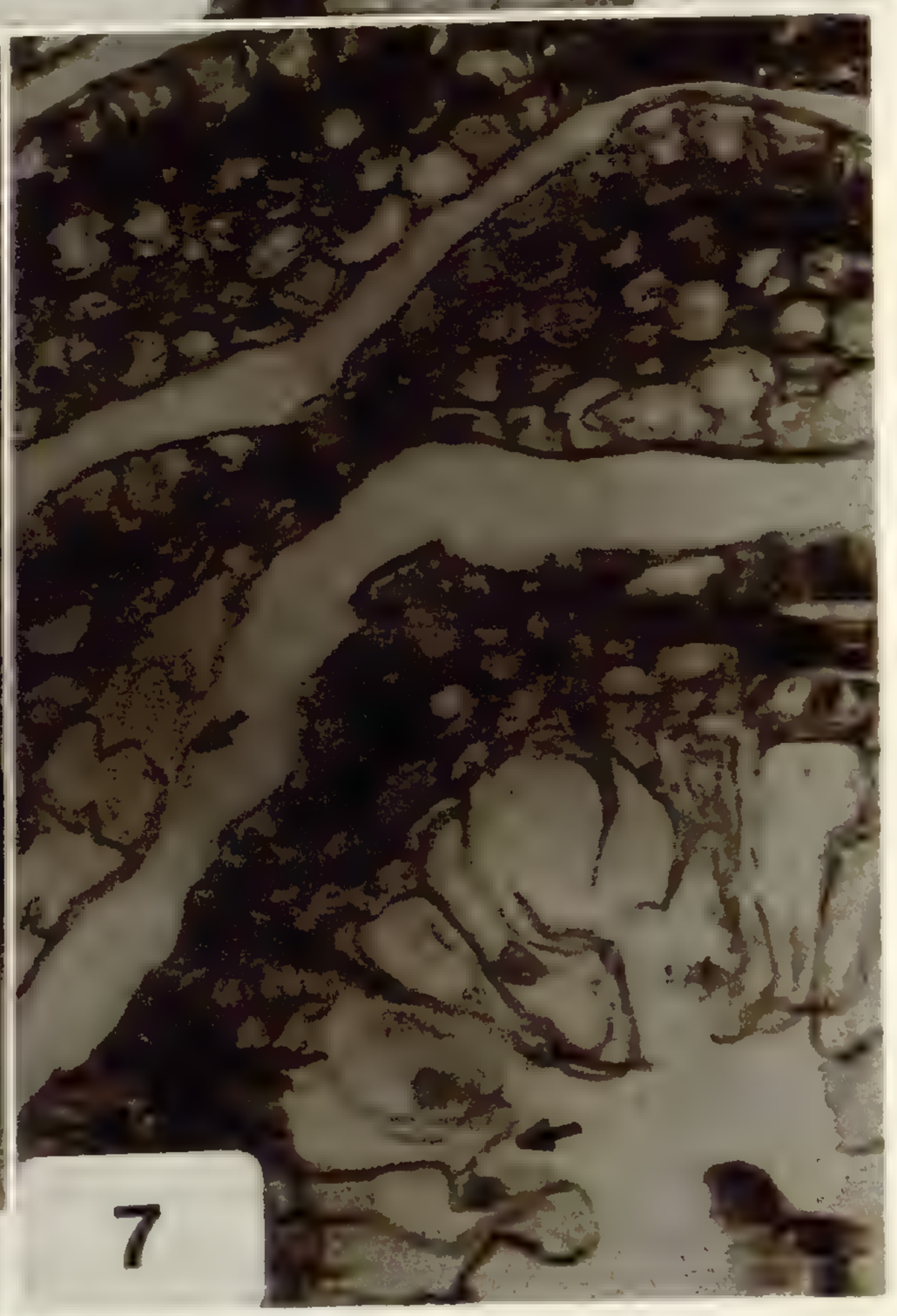
The rhizome buds of *Equisetum* are different from the aerial stem buds in being sharply pointed (Fig. 1) and in having fewer, superimposed sheaths. Rather than the simultaneous development of several internodes, one internode elongates at a time. Roots develop at each node, but branches (rhizome or aerial) develop only occasionally. Numerous nodal buds are initiated, each with a root apical initial and a shoot apical initial. Frequently the root apical initial is functional, while the shoot apical initial generally is dormant or aborts. Occasionally the shoot apical initial becomes active, and the bud subsequently enlarges and erupts through the nodal sheath. Abundant mucilage, apparently produced by the abaxial epidermis, is associated with the rhizome buds, and is particularly obvious when the outermost sheath is dissected from the bud. Those buds destined to produce aerial shoots will possess these same features as they develop at the rhizome node, but change as they grow upward.

The sheath is initiated as a nodal ring, from the upper edge of which a crown of teeth is initiated, grows rapidly upward, and arches over the shoot apex. Then the nodal ring grows upward to produce a sheath consisting of a whorl of segments, one under each tooth, joined laterally by commissures (Hauke, 1985). The adaxial epidermis of the teeth of the rhizome sheath becomes greatly inflated as the teeth elongate and arch over to form a conical cap over the apex (Fig. 3). At first the apical ends of the outer walls of the epidermal cells expand and form papilliform trichomes (Fig. 2), while later the entire cell enlarges and a vertical flange is formed on the adaxial face of the rhizome sheath teeth (Fig. 4). Since the sheath teeth arch inward to form a convex cone the vertical flanges press together to fill the space above the next inner sheath.



FIGS. 1–3. Rhizome buds in *Equisetum*. 1. *E.* ×*schaffneri*. 2. *E. telmateia*, SEM of young sheaths with distinct papilliforme trichomes; scale = 50 μm. 3. *E. arvense*, longisection of bud with overarching sheaths showing expanded adaxial epidermis (arrows); scale = 50 μm.





FIGS. 4–7. Rhizome sheaths in *Equisetum*. 4. *E. arvense*, SEM of sheath with flanges of expanded cells on sheath teeth (arrows); scale = 200 μm. 5. *E. hyemale*, SEM of well-developed trichomes at apices of young sheaths; scale = 200 μm. 6. *E. scirpoides*, longisection of sheath apex with papillae; scale = 50 μm. 7. *E. arvense*, transsection of sheaths with expanded adaxial epidermis (arrows). Scale as in Fig. 6.

Differences exist in the degree of initial outgrowth of the apical end of the epidermal cells, so that in some species there is a more trichome-like appearance of the adaxial epidermis than in others. *Equisetum hyemale* (Fig. 5) shows the most trichome-like appearance of the adaxial epidermis, followed by *E.* ×*schaffneri*, *E. telmateia* (Fig. 2), *E. diffusum*, *E. arvense* (Fig. 3), and *E. scirpoides* (Fig. 6). In the last named species, the epidermal outgrowths are mere papillae. The initial apical expansion is most pronounced in the acropetal cells, and there is a transition in epidermal cell size from highly expanded to normal as one moves from apex to base of a sheath tooth in all species studied (Fig. 3). Thus, in a transverse section showing concentric sheaths, the outer sheaths show less epidermal inflation than the inner ones (Fig. 7). The earliest (i.e., outermost and subsequently lowermost) sheaths on buds destined to become aerial shoots also show rhizomatous features.

Discussion

My observations are consistent with Francini's (1942) description of the expanded inner epidermis of *Equisetum* rhizome sheath teeth. She described the sheath teeth as producing trichomes, which curve upward toward the center of the apex, intertwine, and fill the conical space. According to her, they begin to form in the second sheath from the apex (second youngest sheath), become quite long in the third, and interweave along the axis and develop thickened walls in the fourth sheath. At first I thought that Francini's description of the expanded epidermis was erroneous, because the whole epidermal cell appeared expanded, rather than having a trichome grow from it. The reason for the initial discrepancy between Francini's observations and mine then became obvious, because I could see that initially there was a distinct outgrowth from the upper end of the epidermal cell, followed by a more general expansion of the whole cell. To describe them as trichomes is somewhat misleading. The outgrowths in *E. scirpoides*, *E. arvense*, and *E. diffusum* are more accurately described as papillae, which Uphof (1962) defines as being unicellular, slightly elongated, and little differentiated. Since the structures in *E. telmateia*, *E.* ×*schaffneri*, *E. hyemale*, and probably *E. ramosissimum* are more elongated but still unicellular and little differentiated, they should be referred to as papilliform trichomes. The term "papillenhaare" of Eckhart, or papillate hair, is used for trichomes with a papillose surface (Uphof, 1962) and cannot be used in this case.

The sharply pointed bud ends, expansion of one internode at a time, mucilage production, and expanded adaxial epidermis of *Equisetum* rhizome buds probably all relate to the growth of rhizomes through the ground, and resultant forcing of the apical bud through the soil. The pointedness of the bud could help penetrate the soil. The expansion of one internode at a time would permit a node to complete its development and initiate roots relatively close to the growing point. French (1984) pointed out that the rhizomes of *Equisetum* delay outgrowth of roots and buds from elongating regions of the main axis. This reduces friction and prevents damage to these organs. Also, according to French, a single distal region of

elongation better provides the force for soil penetration than would several active intercalary meristems separated by distances up to several centimeters in length.

The younger sheaths remain enclosed and protected by an older, more indurated sheath for a longer time. The mucilage possibly facilitates the passage of the apical bud through both the oldest enclosing sheath and the soil. The mucilage may also protect the tissues from soil microorganisms. Finally, the expanded adaxial epidermis may, by filling the conical space formed by the enclosing teeth, maintain the sharply pointed form of the sheath as it pushes through the soil, then yield to the next sheath pushing through it.

The rhizome has an apical meristem protected by young leaves. The growing rhizome, subjected to stresses similar to those of a growing root, requires a structure analagous to the root cap for protection against these stresses. In the case of *Equisetum*, the shoot apical bud of a rhizome functions in a similar manner to a root apex. To prevent their being injured by elongation of the root, root hairs do not develop until elongation ceases. Similarly, *Equisetum* nodal roots develop after elongation of the internode below them ceases, and elongation of one internode at a time permits this to occur close to the apex. Mucilage is associated with root apices, and *Equisetum* rhizome buds produce copious mucilage. The root apex forms a root cap, which is continually parting the soil to permit the apex to penetrate, and is continually being replaced by the apex. Similarly, *Equisetum* rhizome apices have a cap of superposed sheaths. These sheaths are sharply pointed to penetrate the soil, are strengthened by the expanded adaxial epidermis, and are continually being grown through by the apex, as well as continually being replaced. Thus the expansion of the adaxial epidermis of the rhizome sheath teeth of *Equisetum* is probably part of the structural adaptation that permits the rhizome to grow successfully in the soil.

Literature Cited

Berlyn, G. P. and J. P. Miksche. 1976. *Botanical microtechnique and cytochemistry*. Ames: Iowa State University Press.

Francini, E. 1942. La struttura dell'apice del rizoma in confronto alla struttura dell'apice del fusto aereo in "*Equisetum ramosissimum*" Desf. Nuovo Gior. Bot. Ital. 49:337–357.

French, J. C. 1984. Occurrence of intercalary and uninterrupted meristems in *Equisetum*. Amer. J. Bot. 71:1099–1103.

Hauke, R. L. 1985. Ontogeny of the commissure of *Equisetum*. Amer. Fern J. 75:111–119.

Sachs, J. 1882. *Textbook of botany*. Translated by S. H. Vines. 2nd Ed. Oxford: Clarendon Press.

Sadebeck, R. 1902. Equisetaceae. Pp. 520–548 in *Die natürlichen Pflanzenfamilien*, 1(4), ed. A. Engler and K. Prantl. Leipzig: W. Engelman.

Uphof, J. C. Th. 1962. *Plant hairs. Handbuch der Pflanzenanatomie* 4(5). Berlin-Nicholassee: Gebrüder Borntraeger.

American Fern Journal 77(2):64–65 (1987)

Schizaea pusilla Discovered in Peru

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Most American pteridologists are familiar with the rare "Curly Grass Fern," *Schizaea pusilla* Pursh, and are aware that it occurs only in scattered localities in northeastern North America. Thus far it has been found (with luck) in southern New Jersey and Long Island, New York, in Nova Scotia and Newfoundland, and on the Bruce Peninsula of Ontario (the latter unconfirmed since the original report, possibly erroneous). Yet recently it has been found on a mountainside in Central Peru! Specimens were collected by Dr. Robin Foster, Research Associate at Field Museum: Peru, Dept. Pasco, Oxapampa, Cordillera Yanachaga, Cerro Pajonal, 12 km SE of Oxapampa, 75°20′W, 20°35′S, 2700–2800 m, *Foster 9065* (F, GH, MO, US, USM); shrubland on white sandstone, spongy sphagnum humus up to 2 m deep except where burned; plant colonizing sandy, wet landslide on steep slope; fertile frond brown, growing with *Drosera* and dwarf *Xyris*.

When Foster presented specimens to me for identification, I remarked that this looked like a new record for Peru, *S. fistulosa* Labill. var. *australis* (Gaud.) Fosb., and set it aside for further study. Later, during research on *Schizaea* in Peru, it became clear that the specimens were instead *S. pusilla*: in the size of the plant, in the number, shape and pubescence of the fertile segments, and as to the character of the spores. The latter were examined by Dr. Alice Tryon on a duplicate collection at GH, who explained (pers. comm.) that spores of this species are quite distinctive in size, shape, and dense pitting of the surface. (For further discussion of the distinctive types of spores in *Schizaea*, see Selling, 1944, and Tryon & Tryon, 1982, pp. 80–82.) The only way the Foster specimens differ from the North American collections is that sterile leaves are not conspicuously curled but are straight to merely flexuous. It is likely that some will consider this single character sufficient basis for specific or infraspecific distinction; however, blade habit can be somewhat variable, even in the Northern plants in which sterile leaves are occasionally flexuous, rarely straight. Actually *S. pusilla* is *not* so closely related to the Old World *S. fistulosa* and its variety *australis* from Chile and Argentina, which differ in the lack of pubescence on the sporangiophore and in the erose-lacerate margins of the fertile ultimate segments. It has greater affinity to *S. incurvata* Schkuhr (Surinam to Venezuela, Peru, northern Brazil), especially in the abundance of long, flexuous trichomes on the subentire fertile segment margins and among the sporangia. *Schizaea incurvata*, however, is a much larger fern, with once- to twice-forked fertile leaves, 2–4 times as many fertile segments, and unpitted spores.

The discovery of *S. pusilla* in Peru prompts interesting speculation as to the true distribution of the species. Should such a "disjunction" really be so surprising? May we not hypothesize that it is to be found in numerous other localities, throughout the neotropics, for example? One has only to attempt a search for it, even in reported stations in the United States, to discover how difficult it

is to locate. Robin Foster reports that his collection was made quite by accident, when he slipped and fell traversing the landslide area, only to find this strange little fern virtually "under his nose." Even then, only careful scrutiny produced a dozen more plants. How many more inconspicuous ferns can we expect to encounter in the tropics—either by luck or through assiduous search—such as species of Hymenophyllaceae and Ophioglossaceae? Even the larger *Schizaea incurvata* has been reported but once from Peru. Obviously, awareness of special soil requirements or habitat preferences can increase the likelihood of finding certain rare ferns. North American collection reports inform us that *S. pusilla* usually is found "in wet, sandy areas" and "in sphagnous bogs"; and the Foster collection proved no exception to this. That is not to say the fern is not found in other, e.g., drier or rocky habitats, but according to Selling (p. 81, 1944): "It is distinctly a species which prefers moisture and acid soils." By their very nature, general and mass collecting expeditions will yield but a small percentage of such fortunate discoveries; but special awareness and advance preparation can raise the odds!

Literature Cited

Selling, O. H. 1944. Studies in the recent and fossil species of *Schizaea*, with particular reference to their spore characters. Acta Horti Gothob. 16:1–112.

Tryon, R. M. and A. F. Tryon. 1982. *Ferns and allied plants, with special reference to tropical America*. New York: Springer-Verlag.

Review

"*Illustrations of Pteridophytes of Japan, Volume 4*," edited by S. Kurata and T. Nakaike with the cooperation of the Nippon Fernist Club. 1985. x + 852 pp. + folding map. University of Tokyo Press. Yen 13,000. ISBN 4-13-061064-3.

The hundred pteridophytes depicted in volume four of this ongoing series bring us to the halfway point in coverage of the perhaps 800 Japanese taxa. The format of previous volumes, all previously reviewed (Amer. Fern J. 72:11, 1982; 72:48, 1982; 74:6, 1984) is faithfully followed.

Among genera wholly or partly contained in this volume are *Angiopteris*, *Bolbitis*, *Cyathea*, *Dryopteris* (31 species and varieties), *Equisetum*, *Gymnocarpium*, *Plagiogyria*, *Pteris*, *Tectaria*, and *Woodsia*. I noted an error in the spelling of *Pteris dispar* Kunze, a species whose two cytotypes were intensively studied and mapped by N. Nakato in J. Jap. Bot. 56:200–205, 1981. The tetraploid is northern, with larger spores and smaller scales than the diploid. Some authors have treated *dispar* as a variety of *Pteris semipinnata* L.—M. G. Price, Herbarium, North University Building, University of Michigan, Ann Arbor, MI 48109.

American Fern Journal 77(2):66–72 (1987)

Shorter Notes

Chromosome Numbers of Some Ferns from Argentina.—This contribution is a part of fern projects in progress, namely the systematic revision of the Argentine Thelypteridaceae (by M. Ponce) and a study of the *Microgramma squamulosa* group in the Neotropics (by E. de la Sota and L. Cassá de Pazos).

Material of *Thelypteris* was fixed in situ; *Microgramma* was fixed from plants from Tucumán under cultivation. All material was fixed in Newcomer fluid modified by Hunziker (Kurtziana 3:151–156, 1966). Traditional cytological procedures were utilized for *Thelypteris*. Root tips of *Microgramma squamulosa* were pretreated with 0.002 M 8-hydroxyquinoline for about 3 hours at room temperature. Both types of material, somatic and gametic, were stained with Feulgen and hematoxylin. Photomicrographs were taken with a Zeiss microscope and a Zeiss-Ikon camera. Voucher specimens are deposited in LP and SI.

Results can be summarized as follows:

Microgramma squamulosa (Kaulf.) Sota (Fig. 1,A–D). $2n = 74$, root tips; $2n = 37$ II, meiosis regular. Argentina, Tucumán, Ciudad de Tucumán, Jardín Fundación Miguel Lillo, *Legname* s.n. (LP); under cultivation in Villa Lugano, ciudad de Buenos Aires.

Thelypteris (§*Amauropelta*) *stierii* (Rosenstock) Reed (Fig. 1F) $2n = 29$ II, meiosis regular. Argentina, Salta, Depto. Anta, Parque Nacional "El Rey," picada al Chorro de los Loros, Río La Sala, *Ezcurra et al. 425* (SI).

Thelypteris (§*Goniopteris*) *abbiattii* Reed (Fig. 1E). $2n = 36$ II, meiosis regular. Argentina, Buenos Aires, Isla Martín García, Barrio Chino, *Tur et al. 1825* (LP, SI).

At present, chromosome numbers of nine species of *Microgramma* are known. Most are based on $x = 37$, but Smith and Foster (Fern Gaz. 12:321–329, 1984) and Evans (Caryologia 16:671–677. 1963), reported $n = 36$ for *Microgramma vacciniifolia* (Langsd. & Fisch.) Copel., while Sota and Cassá de Pazos (Bol. Soc. Argent. Bot. 19:69–73, 1980) gave $n = 37$ for the same species. The gametic and somatic numbers reported here for *M. squamulosa* and before for *M. vacciniifolia* support the hypothesis that these taxa are the parents of *M. mortoniana* Sota, as was previously presumed (de la Sota, Amer. Fern J. 63:61–64, 1973).

Additional counts on *Microgramma vacciniifolia* are desirable. That taxon and *M. squamulosa* appear to be part of a complex. Attention should also be paid to the seasonality of spore production. This might help explain strong meiotic abnormalities noticed by Smith and Foster (*l.c.*) for *Microgramma lindbergii* (Mett. ex Kuhn) Sota and *M. vacciniifolia*. Thus, autumnal spores of *M. mortoniana* showed a low germinative power and a high content of oily components (de la Sota & Cassá de Pazos, *l.c.*).

This contribution was partially supported by Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina (CONICET), grant no. 17745A/84. Results were given during the Session of Cytology of the XX Jornadas

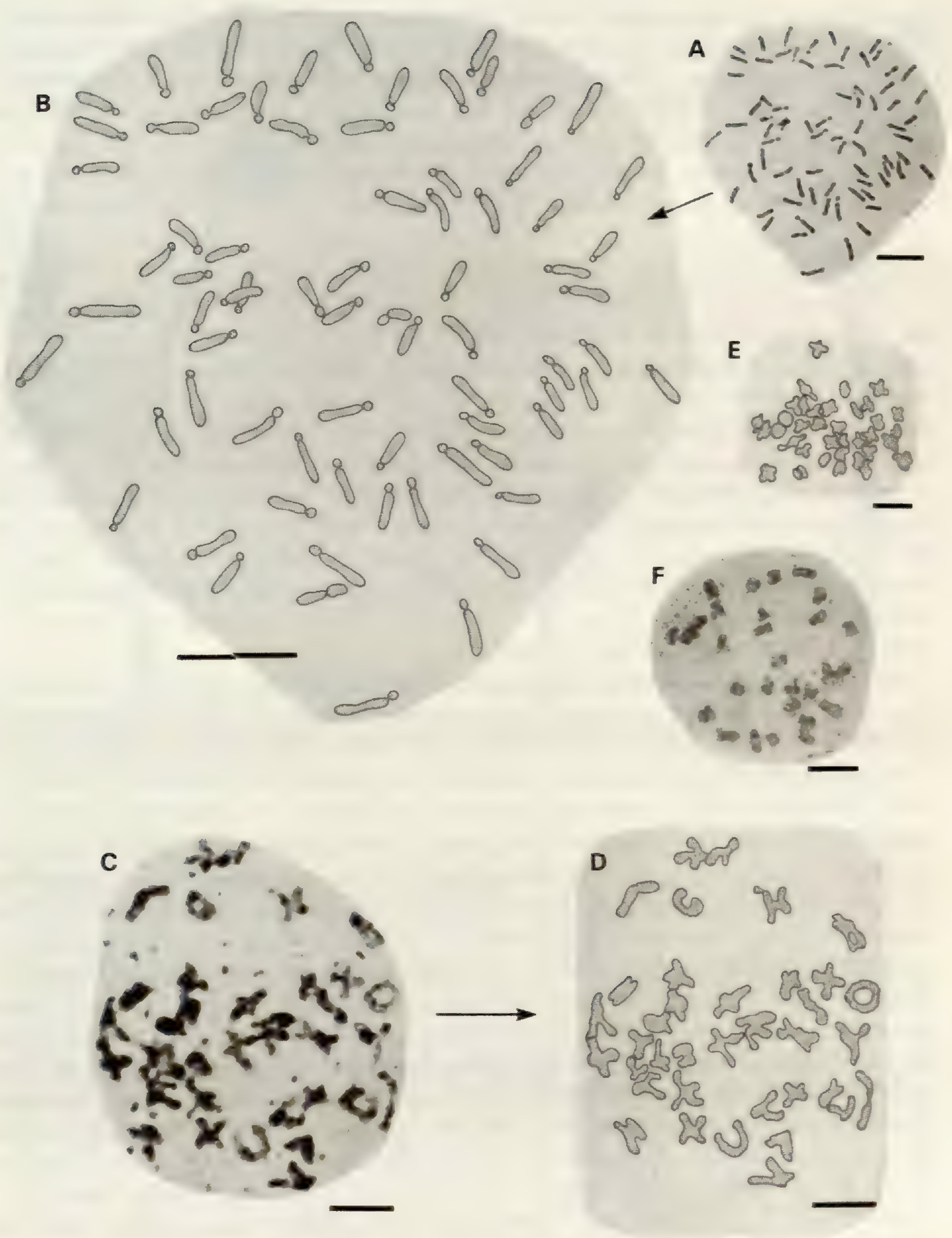

FIG. 1. Chromosomes of Argentine ferns. A, root tip mitosis in *Microgramma squamulosa*, showing 74 somatic chromosomes; B, drawing of the same configuration; C, meiosis in *M. squamulosa*, showing 37 bivalents; D, drawing of the same configuration; E, drawing of metaphase I in *Thelypteris abbiattii*, showing 36 bivalents; F, metaphase I in *Thelypteris stierii*, showing 29 bivalents. Bar scales = 10 μm.

Argentinas de Botánica, ciudad de Salta, 16–20 September 1985. We acknowledge the economic help given by CONICET and the technical assistance of Víctor H. Calvetti.—Elías R. de la Sota, División Plantas Vasculares, Facultad Ciencias Naturales y Museo, UNLP, Paseo del Bosque, 1900 La Plata, Argentina; Marta Mónica Ponce, Instituto de Botánica Darwinion, Labardén 200, C.C. no. 22, 1642 San Isidro, Argentina; Liliana A. Cassá de Pazos, Instituto Fitotécnico Santa Catalina, Facultad de Agronomía, UNLP, C.C. no. 4, 1836 Lavallol, Argentina.

***Botrychium pinnatum* in Colorado.**—Western North America has been found to be a center of distribution for the moonworts, *Botrychium* subg. *Botrychium*, with 13 species and several hybrids (Wagner & Wagner, Amer. Fern J. 73:53–62, 1983; Wagner & Wagner, Amer. Fern J. 76:33–47, 1986). The mountains of Colorado have proven to be rich in both species and localities. It is possible to find four or even five species growing together in a roadside meadow in the subalpine zone, as was demonstrated in the 1984 Annual Fern Foray on Mt. Evans, led by the Wagners and ourselves. Although the state has been the scene of intense botanical activity, most attention has been focused on the state's spectacular alpine flora. Botrychiums have been collected only incidentally until recently, when they became the subject of study.

On 30 July 1986, while traveling north on US Rt 550 just south of Coal Bank Pass, near the southern boundary of San Juan County, one of us (J.D.M.) noted that we were passing what could be good *Botrychium* habitat. We stopped and examined a small dry drainage channel at the edge of an Engelmann spruce forest. Elevation was approximately 3045 m (10,000 ft). In a short time approximately twelve plants were found of a *Botrychium*. These were identified as *B. pinnatum* St. John, using the keys in Lellinger (*A field manual of the ferns & fern allies of the United States & Canada*, 1985) and Wagner and Wagner (1986). Specimens have been identified also by W. H. Wagner Jr. (pers. comm.). Silhouettes of this collection, *Montgomery & Root 86-279*, are illustrated in Figure 1. The similarity in vegetative blade and pinna shape and margin with the illustrations in Wagner and Wagner (1983, fig. 1, e–g) is striking and also confirms our identification. These plants were growing in a relatively dense growth of low herbs in contrast to the more open habitat such as roadsides where Colorado moonworts are usually found. In drier gravel near the roadside one plant of *B. lanceolatum* and two of a possible *B. lanceolatum* × *pinnatum* hybrid were found. The possible hybrids have been sent to W. H. Wagner Jr. for further study. Specimens of *B. pinnatum* have been deposited at COLO and MICH. The collection has also been reported to the Colorado Natural Areas Program and is being considered for listing under plants of special concern for the state.

Weber (*Rocky Mountain flora*, 1976) listed *B. boreale* Milde, a Eurasian species formerly confused with *B. pinnatum* (Wagner & Wagner, 1983) as occurring in Colorado. This record is apparently based on a specimen (*Willard & Porsild 6062*, COLO) from Rocky Mountain National Park in Larimer County. Recent examination of this specimen has shown that it is probably *B. hesperium* (Maxon &

FIG. 1. Silhouettes of leaves of *Botrychium pinnatum* from Coal Bank Pass, Colorado (*Montgomery & Root 86-279*).

Clausen) Wagner & Lellinger. The specimens collected from San Juan County are thus the first verified record of *B. pinnatum* in Colorado. This represents a range extension to the south from the range reported by Lellinger (1985) as Alaska to the mountains of Montana, northern Nevada, and Oregon. Ranges of most moonworts are subject to revision as these small and inconspicuous plants become better understood and pteridologists become more familiar with their habitats. We observed additional potential habitats for moonworts on both Coal Bank Pass and Molas Divide. The San Juan Mountains are a geologically complex area of southwestern Colorado which is largely inaccessible and has not been thoroughly explored botanically; future examination of this area by pteridologists is certainly warranted.—PETER G. ROOT, Kathryn Kalmbach Herbarium, Denver Botanic Gardens, 909 York St., Denver, CO 80206, and JAMES D. MONTGOMERY, Ecology III, Inc., R.D. 1, Berwick, PA 18603.

New Records of Pteridophytes from the State of Chiapas, Mexico.—As a result of intensive field work for the Flora Mesoamericana Project, several species of pteridophytes must be added to those already known for the State of Chiapas. Some of them were expected (Smith, *Flora of Chiapas, part 2: Pteridophytes,*

1981; Breedlove, *Listados florísticos de México, IV, Flora de Chiapas,* 1986) because they grow at low elevations in the Eastern Highlands and in the eastern part of the Central Plateau of the state. These floristic associations are continuous with associations in the Petén region of Guatemala. Five out of ten new records are filmy ferns, which are easily overlooked because of their small size and because often they grow mixed with other species of Hymenophyllaceae.

In this paper information is given to distinguish the species from related species already reported from Chiapas. Identifications have been made or verified by Ramón Riba and Leticia Pacheco.

Actinostachys germanii Fée—Mpio. Ocosingo, Crucero Corozal on the road Palenque-Boca Lacantún, 180 m, semi-evergreen seasonal forest (periodically inundated), 6 Nov 1985, *E. Martínez S. 14891,* MEXU, UAMIZ. It differs from *Schizaea* by the sterile leaf which is simple and linear, similar to a small slender grass; sporangiophores are digitate. The plant is inconspicuous and is easily overlooked in the field.

Grammitis minuscula (Maxon) Copel.—Mpio. La Trinitaria, Lagos de Montebello, 1450 m, pine-oak-Liquidambar forest, 7 Aug 1984, *L. Pacheco 1300,* UAMIZ. It differs from the other Chiapan species of *Grammitis* by the entire elliptical leaves and round sori. The only difference between *Pacheco 1300* and the original description is that the specimen is a little shorter, probably due to the degree of exposure of the plant.

Lindsaea portoricensis Desv.—Mpio. Ocosingo, 10 km S of Ejido Benemérito de las Américas, on road to Flor de Cacao, Marqués de Comillas, 120 m, semi-evergreen seasonal forest, 9 Dec 1984, *E. Martínez S. 9508,* MEXU, UAMIZ. This differs from the other species of *Lindsaea* in Chiapas by the brownish red, abaxially terete stipe, pinnae strongly ascendent, almost vertical and touching each other, and pinnules subrectangular, 1.5–2 times as long as wide.

Schizaea poeppigiana Sturm—Mpio. Ocosingo, Crucero Corozal on the road Palenque-Boca Lacantún, 180 m, in semi-evergreen seasonal forest (periodically inundated), 8 Jan 1986, *E. Martínez S. 15618, 15673,* MEXU, UAMIZ. This differs from *Schizaea elegans* by the dimorphic leaves, the fertile leaves not foliose, its fertile axis strongly recurved at maturity; sterile leaves repeatedly furcated, the divisions not or very slightly expanded and joined only at the base. The species has been reported only for the Bahamas, Greater Antilles and from Costa Rica to the Guianas and Peru.

Thelypteris falcata (Liebm.) Tryon—Mpio. Ocosingo, 2 km S of Crucero Corozal, on road Palenque-Boca Lacantún, 180 m, semi-evergreen seasonal forest (periodically inundated), 21 Sept 1984, *E. Martínez S. 7675,* MEXU, UAMIZ. It differs from *T. standleyi* by its sporangial stalks without hairs and secondary veins nearly straight, not arcuate or subsigmoid.

Trichomanes ekmanii W. Boer—Mpio. Pichucalco, 6 km N of Pichucalco (by air), 200 m, old secondary growth in tropical rain forest, wet creeks, 18 Feb 1985, *A. Espejo 1440* & *S. Hernández,* UAMIZ. This differs by the small blades with a continuous submarginal false vein and without marginal hairs; cross-veins wanting; involucres immersed, without lips and not dark-edged.

Trichomanes godmanii Hooker—Mpio. Ocosingo, Crucero Corozal on road

Palenque-Boca Lacantún, 180 m, semi-evergreen seasonal forest, 23 Feb 1985, *E. Martínez S. 11101,* MEXU, UAMIZ. This differs from *T. ekmanii* by the abundant false veins, these parallel and perpendicular to the true veins, the venation appearing reticulate.

Trichomanes holopterum Kunze—Mpio. Ocosingo, Crucero Corozal on road Palenque-Boca Lacantún, 220 m, semi-evergreen seasonal forest (periodically inundated), 6 Nov 1985, *E. Martínez S. 15009,* MEXU, UAMIZ. This differs from *T. crispum* by the winged petiole, shorter blades, broadly winged rachis, and few (5–10) segments on a side. The species has been reported previously only for the Greater and Lesser Antilles.

Trichomanes membranaceum L.—Mpio. Ocosingo, 6 km NE from Pichucalco (by air), 220 m, old secondary growth in tropical rain forest, 18 Feb 1985, *A. Espejo 1441 & S. Hernández,* UAMIZ. The species can be easily separated from the others of subg. *Didymoglossum* by the simple or slightly lobed blade, false veins parallel to the true veins, and by the paired orbicular scales in the margin of the blade.

Trichomanes tuerckheimii Christ—Mpio. Ocosingo, Nuevo Veracruz, 33 km W of Rio Chixoy, road to Chajul, Marqués de Comillas, tropical deciduous forest, 10 Jan 1986, *E. Martínez S. 15908,* MEXU, UAMIZ. It is distinguished from *T. pinnatum* by the long-creeping rhizome, distant subsessile leaves, false veins few, located near the margin and parallel to the true veins, and by "prehensile" trichomes on veins, midribs, and margins in the abaxial face of the blade, which cause the lamina to adhere to the surface of the host plant.—RAMÓN RIBA and LETICIA PACHECO, Depto. de Biología, C.B.S., Universidad Autónoma Metropolitana-Iztapalapa, Ap. Postal 55-535, México, D. F. 09340; and ESTEBAN MARTÍNEZ S., Depto. de Botánica, Instituto de Biología, UNAM, México, D. F. 14020.

Additions to the Fern Flora of the Bahamas.—The publication of Correll and Correll's (1982) *Flora of the Bahama Archipelago* has significantly improved our understanding of the Bahamian flora and, as is the case with any new flora, has stimulated the discovery of corrections and new taxa. As part of a study of the phytogeography of the Bahamian archipelago, I encountered several specimens that represent additions to the flora.

Hypolepis repens (L.) Presl.—This taxon represents a new genus and species for the Bahamas. It occurs on the islands of Grand Bahama (*Correll & Kral 42936,* FTG), New Providence (*Correll & Correll 48320,* FTG), North Andros (*Correll & Proctor 47828,* FTG), and San Salvador (*Correll & Wasshausen 46861,* FTG). All four collections are sterile, and this has apparently confounded identification by D. S. Correll who annotated two of the sheets as young plants of *Pteridium aquilinum* var. *caudatum.* The Grand Bahama collection consists of very young plants (less than 1.5 dm tall) and would not be placed as *H. repens* except for the presence of other more readily identifiable specimens for comparison. The occurrence of the species in the Bahamas is not especially surprising in light of its wide range in the West Indies and the Florida peninsula (cf., Proctor, *Flora of the Lesser Antilles. Vol. 2. Pteridophyta,* 1977). The plants occur in forested

areas (coppice, pineland, or *Casurina* thickets) in or around ponds or depressions. The lack of apparently suitable habitats (based on populations outside of the Bahamas) may account for the species' restriction to larger islands where suitable habitats are more likely to exist. Additionally, the occurrence near the more populated portions of the islands and the fact that the collections are more recent than 1974 suggest that *H. repens* may represent an escaped cultigen. This will be a difficult proposition to test given the species' wide geographic range and the probability that cultivated plants may also have originated in Florida, Cuba, or Hispaniola.

Polypodium polypodioides (L.) Watt var. *michauxianum* Weatherby.—Correll and Correll (1982) reported only the typical variety for the Bahamas, but several specimens of var. *michauxianum* have been discovered. The variety is here reported as new to the flora. It occurs only on Great Abaco (*Correll et al. 42651*, FTG; *Correll & Meyer 44540, 44590, 44609*, all FTG). All of the collections were from ledges, rocks, or logs in dense coppice vegetation.

Pteris × *delchampsii* Wagner & Nauman.—This hybrid between *P. vittata* L. and *P. bahamensis* (Agardh) Fée occurs on the island of Grand Bahama (*Correll 50507*, FTG). The collection is from a single clump in a shaded sinkhole in open pinelands, a habitat typical of Florida populations. The plant's occurrence in the Bahamas was to be expected since both parental taxa also occur there.

Thelypteris hispidula (Decne.) Reed var. *versicolor* (R. St. John) Lellinger.—This species is here reported as new to the Bahamian flora. It occurs on North Andros (*Hill 3032*, FTG) and Mangrove Cay (*Popenoe 228*, FTG). Both collections are from sinkholes in habitats dominated by pine. Suitable habitat exists elsewhere in the Bahamas and this species is expected to spread.—CLIFTON E. NAUMAN, Fairchild Tropical Garden, 10901 Old Cutler Road, Miami, FL 33156.

Announcement: 1988 AIBS Meeting

The annual meeting of the American Fern Society will be held in conjunction with the American Institute for Biological Sciences on August 14–18, 1988, at the University of California, Davis. Persons wishing to present talks should contact Dr. Judith Skog, Biology Dept., George Mason University, Fairfax, VA 22030, before 15 January 1988 for information.

A Fern Foray to Bear Valley, Point Reyes Peninsula, will take place on Saturday, 13 August 1988. A second trip will be to the University of California Botanical Garden and the Tilden Park Botanical Garden on Sunday, 14 August. Many native ferns, including *Blechnum spicant, Dryopteris expansa, Polypodium* spp., *Aspidotis* spp., and *Pellaea* spp. will be seen during the two days. Trips will leave from Davis and be restricted to 45 people. No collecting will be permitted. Leaders are Alan Smith, Don Macneill, and Tom Lemieux. For more information, contact Smith at (415) 642-7890.

INFORMATION FOR AUTHORS

Authors are encouraged to submit manuscripts pertinent to pteridology for publication in the *American Fern Journal.* Manuscripts should be sent to the Editor. Acceptance of papers for publication depends on merit as judged by two or more referees. Authors are encouraged to contribute toward publishing costs; however, the payment or non-payment of page charges will affect neither the acceptability of manuscripts nor the date of publication.

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Papers longer than 32 printed pages may be sent to the Editor of *Pteridologia* (Memoir Editor, see cover 2).

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The editors (Dennis Wm. and Jan Wassmer Stevenson) welcome contributions from members and non-members, including miscellaneous notes, offers to exchange or purchase materials, personalia, horticultural notes, and reviews of non-technical books on ferns.

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Mr. Neill D. Hall, 1230 Northeast 88th Street, Seattle, WA 98115, is Director. Spores exchanged and lists of available spores sent on request.

Gifts and Bequests

Gifts and bequests to the Society enable it to expand its services to members and to others interested in ferns. Botanical books, back issues of the Journal, and cash or other gifts are always welcomed, and are tax-deductible. Inquiries should be addressed to the Secretary.

American Fern Journal 77(3):73-89 (1987)

An Introduction to the Pteridophyte Flora of Finca La Selva, Costa Rica

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Finca La Selva, now more properly known as the La Selva Biological Station, is the flagship field station of the Organization for Tropical Studies (OTS) in Costa Rica. A comprehensive floristic inventory of La Selva was initiated in 1979 (Hammel & Grayum, 1982), and a technical flora has recently begun to appear in fascicle form in the journal *Selbyana* (see Wilbur, 1986). The recent completion of the pteridophyte treatments for this flora (Grayum & Churchill, 1988a, 1988b; here summarized in Appendix 1) permits the present informal introduction and analysis.

THE SITE

Finca La Selva is located in the Caribbean lowlands of Costa Rica, in the zone where the volcanic Central Cordillera begins to rise up out of the swampy coastal plain. The Station occupies 1533 hectares at the confluence of the Ríos Puerto Viejo and Sarapiquí. The elevation on the property ranges from about 35 m (where the rivers meet) to 130 m on the higher ridges toward the South Boundary. Recent alluvial soils occur along the rivers and lower portions of the major quebradas (creeks), but volcanically derived soils predominate elsewhere. The major habitat at La Selva is upland primary forest; however, several other habitats are represented, including swamp forest, open marshes, streamsides and riparian forest, alluvial forest, secondary forest, and weedy areas (see Appendix 1).

La Selva lies in one of the wettest parts of Costa Rica, receiving an average of about 3900 mm of rain per year. Although there is a slight dry season from January through April, it is not nearly so pronounced as that experienced on Costa Rica's Pacific slope during these months.

More detailed descriptions and additional information can be found in numerous other sources (e.g., Grayum, 1982; Hartshorn, 1983; Hammel, 1986; Wilbur, 1986).

HISTORY OF PTERIDOPHYTE COLLECTING AT LA SELVA

The earliest known pteridophyte collections from on or very near the site now known as La Selva were made during the "Golden Period" of Costa Rican natural history (see Gómez & Savage, 1983), around the turn of the century. Pablo Biolley and Henri Pittier, Swiss botanists based in San José, visited the "confluence of the Río Puerto Viejo and Sarapiquí" at least twice, in April, 1892 and February,

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1893, making general plant collections. Among the ferns collected by Biolley and Pittier were two species, *Pteris quadriaurita* and *Pityrogramma tartarea*, that have not since been recollected from La Selva.

During most of the first half of the present century, natural history languished in Costa Rica for a variety of reasons (Gómez & Savage, 1983), and little or no botanical fieldwork was undertaken in the La Selva vicinity. The next pteridophyte collections on record from La Selva are those of Edith Scamman, a fern specialist associated with Harvard's Gray Herbarium, who visited Costa Rica in 1951, 1953, 1955, and 1956, amassing a total of about 1400 specimens (Tryon & Tryon, 1968). Herbarium labels indicate that Scamman collected ferns at La Selva (then the property of Dr. Leslie R. Holdridge) on at least one occasion, from 18–28 February 1955; however, the exact number of specimens collected at the site is difficult to establish from this source.

By 1967 Finca La Selva had become OTS property, and in the summer of that year OTS conducted a field course on the biology of tropical pteridophytes in Costa Rica (Mickel, 1967). This course was coordinated by Dr. John T. Mickel, and included Drs. Elías de la Sota, Warren H. Wagner, Jr., A. Murray Evans and David B. Lellinger as full- or part-time faculty. The list of participants in the course, including "ten outstanding students . . . selected from nine universities across the United States," now reads like a "Who's Who in American Pteridology." During a few days at La Selva in mid-August, this group produced the first checklist of La Selva pteridophytes (OTS, 1967), accounting for 89 of the 173 species presently known. De la Sota (1971) later published a list of the 56 epiphytic species then known from La Selva.

During the interval from 1967 to 1979, minor pteridophyte collections were made at La Selva by individuals too numerous to mention, including many of those involved in the 1967 course. The Costa Rican pteridologist Luis Diego Gómez visited the site on many occasions, making several significant collections and compiling a checklist, circulated by OTS during the mid- and late 70s, that enumerated 100 pteridophyte species. From March to September of 1978, the first author made numerous collections of pteridophytes and other groups at La Selva.

The "Flora of La Selva" project was officially inaugurated in 1979, and in the summer of that year the first author worked as the first collector for that project. Intensive general collecting was pursued at La Selva from that time until about 1985, and collecting continues, albeit spottily, to the present. A number of collectors have been involved in this effort, chief among them Barry Hammel, Robert L. Wilbur, James Folsom, Tim McDowell, Brian Jacobs, Isidro Chacón, Damon Smith, and John Sperry. The first set of this material is deposited at DUKE.

In March, 1985, June Barcock prepared approximately 100 fern specimens during the visit of "Operation Raleigh" to La Selva. This collection, deposited at Kew, is significant in that it was made in a poorly explored area of the property; moreover, some specimens were obtained from the canopy by means of a platform constructed by the group. In addition to several rare species, two species new to the flora (*Trichomanes crispum* and *Blechnum polypodioides*) were collected.

TABLE 1. Total Number of Pteridophyte Species in Selected Floras.

Place	Area (km²)	Pterid. spp.	Authority
California	411,013	86	Grillos, 1966
Texas	692,405	107	Correll, 1956
Chihuahua	245,612	126	Knobloch & Correll, 1962
Florida	151,670	135	Lakela & Long, 1976
Zambia	752,614	146	Kornaś, 1979
La Selva	**15**	**173**	**Grayum & Churchill, 1988a, b**
Hong Kong	1,034	175	Edie, 1978
Puerto Rico	8,897	263	Kepler, 1975
Australia	7,686,849	416	Jones & Clemesha, 1981
Jamaica	10,962	579	Proctor, 1985
Chiapas	ca. 74,000	609	Smith, 1981
Costa Rica	50,900	ca. 900	Grayum, unpubl. data

THE PTERIDOPHYTE FLORA: GENERAL REMARKS

At the present time, 173 species of pteridophytes in 45 genera are known from Finca La Selva, ranking this tiny site respectably high among several much larger political units (see Table 1) selected more or less randomly on the basis of ease of extraction of comparable data. Seven additional species, including one additional genus (*Dicranopteris*), have been collected immediately adjacent to La Selva and have been considered likely hypotheticals and treated in full for the Flora. Two further species, *Antrophyum lineatum* and *Grammitis turrialbae*, are vouchered for La Selva by a single correctly identified specimen each; however, both are mid- to high-elevation species and label mixups are strongly suspected.

Particularly surprising is the comparison of the La Selva pteridoflora with that of Florida (Table 1), the most tropical of the continental 49 states and about 10,000 times the size of La Selva, but with 21.5% fewer pteridophyte species.

In view of the thoroughness with which La Selva has been botanically inventoried, the above figures probably represent a reasonably close approximation of the actual totals. Clearly, however, they are not exact, nor can we ever hope to make them so. Although the area of La Selva is quite small, the terrain is rugged and complex. Large areas of the reserve are inaccessible by trail, and most of these have been only cursorily explored. Certain parts of the so-called "Western Annex," added to La Selva in 1982, remain completely unexplored.

More intensive collecting along creeks and on ridges in the more remote and relatively poorly explored southern portions of La Selva will certainly yield new fern records (as demonstrated by the Barcock effort discussed previously). This seems especially likely when one considers the highly localized distribution patterns characteristic of many plant species in the La Selva rain forest, contrary to what one might predict of this superficially uniform environment. For example, 33 (about 19%) of the 173 pteridophyte species presently known from La Selva are classed as "very rare" (known from just one or two collections; see Appendix 1), including such conspicuous ferns as *Metaxya rostrata* and *Thelypteris gigan-*

tea; an additional 45 species (26% of the total) are considered rare (known from 3–5 collections). Thus about 45% of the La Selva fern flora consists of species unlikely to be encountered by the short-term visitor (interestingly, roughly the same fraction unaccounted for by the 1967 course). These figures are surprising in view of the "notorious" ease with which fern spores are dispersed in the air (Smith, 1972; Gentry & Dodson, 1987); however, comparable numbers for the likewise air-dispersed Orchidaceae at La Selva may be higher yet (J. Atwood, pers. comm.). Hammel (1986) reported that about 75% of the La Selva species in six angiosperm families with more conventional seed-dispersal modes "are known from a few individuals or from a few small populations."

The inherently dynamic nature of natural floras presents an additional obstacle to a precise inventory of the La Selva pteridophytes. Certain habitats seem especially subject to ostensibly temporary colonization by basically extralimital species, pteridophytes and spermatophytes alike. Such habitats include recently disturbed or weedy sites in primary or secondary forest and, especially, the banks of the Ríos Puerto Viejo and Sarapiquí, regularly disturbed by landslides and diaspore-bearing floodwaters. The distribution at La Selva of species such as *Blechnum fraxineum*, *Dennstaedtia cicutaria*, and *Thelypteris resinifera* suggests ephemeral occurrence in the latter habitat. This may also be the case with *Pityrogramma tartarea* and *Pteris quadriaurita*, not recollected in the La Selva vicinity for nearly a century.

The air-dispersed diaspores of pteridophytes perhaps render the La Selva pteridophyte flora more dynamic than the spermatophyte flora. This is suggested by recent discoveries of species new to the flora in heavily collected sites, e.g., *Stigmatopteris longicaudata* along the Quebrada El Taconazo and, most dramatically, *Ophioglossum reticulatum* in the laboratory clearing.

A particularly striking feature of the La Selva fern flora that is also probably attributable to the high vagility of air-dispersed plants is the dearth of undescribed species. In fact, just one La Selva pteridophyte species (an *Elaphoglossum*) is believed to be new to science (although a few others, such as *Diplazium pactile* and *D. striatastrum*, were described within the last decade). Similarly, only a single La Selva orchid species (out of 113) is apparently undescribed (J. Atwood, pers. comm.). This is markedly in contrast with the situation for spermatophytes in general: for example, 12 (about 10%) of the 123 species in the subset of six angiosperm families analyzed by Hammel (1986) were described by Hammel himself, and over 50 new species of seed plants have been described from La Selva altogether (Wilbur, 1986).

The La Selva pteridoflora also includes but two apparent country records (*Danaea grandifolia* and *Bolbitis aliena*), contrasting with the spermatophyte flora (Grayum & Hammel, 1982) in this respect as well.

Before proceeding with the analysis of the La Selva pteridoflora, an important taxonomic qualification is necessary. The number of pteridophyte genera attributed to La Selva and (to a lesser extent) the number of species depends on one's taxonomic viewpoint. Pteridophytes are notoriously intractable as regards familial and generic classification. For the purposes of the La Selva flora, rather broad circumscriptions were opted for in most cases. Without narrowing these very

TABLE 2. Most Diverse Pteridophyte Genera at Three Neotropical Sites.

LS[1]		BCI		RP	
Genus	Spp.	Genus	Spp.	Genus	Spp.
Thelypteris	18	*Polypodium*	13	*Thelypteris*	11
Polypodium	17	*Trichomanes*	9	*Polypodium*	7
Trichomanes	14	*Adiantum*	9	*Adiantum*	6
Asplenium	11	*Thelypteris*	8	*Asplenium*	5
Selaginella	9	*Selaginella*	6	*Diplazium*	5
Tectaria	9	*Asplenium*	6	*Tectaria*	4
Diplazium	8	*Pteris*	4	*Selaginella*	3
Adiantum	7	*Elaphoglossum*	3	*Trichomanes*	3
Elaphoglossum	6			*Elaphoglossum*	3
				Stigmatopteris	3

[1] Acronyms and data sources: LS = La Selva (Grayum & Churchill, 1988a, b); BCI = Barro Colorado Island (Croat, 1978); RP = Río Palenque (Dodson & Gentry, 1978).

radically, well over a dozen pteridophyte genera (e.g., *Lycopodiella, Huperzia, Trichipteris, Megalastrum, Peltapteris, Cochlidium, Olfersia, Campyloneurum, Phlebodium, Microgramma, Niphidium, Pecluma, Pleopeltis, Christella, Goniopteris, Macrothelypteris, Meniscium, Ananthacorus*) could be added to the La Selva total of 45. An additional species could be appended, raising the total to 174, were *Asplenium auritum* recognized as distinct from *A. cuspidatum* (both entities occur at La Selva).

COMPOSITION OF THE FLORA

Of the 173 La Selva pteridophyte species, 160 (in 43 genera) belong to the Divison Polypodiophyta and 127 (in 35 genera) to the broadly-circumscribed Polypodiaceae, including three weedy species introduced from the Old World (*Nephrolepis multiflora, Thelypteris dentata*, and *T. torresiana*). Polypodiaceae thus reigns as the largest family in the La Selva vascular flora, surpassing the largest angiosperm family, Orchidaceae, which comprises 113 species (and two fewer genera; Atwood, 1986). Furthermore, ferns are conspicuously more abundant than orchids (from an understory perspective, at any rate). Pteridophyte species account for about 9% of the La Selva vascular flora (based on an estimated total of 1900 species; see Wilbur, 1986), which falls in the range of 5–10% given by Smith (1981) for wet tropical forests.

The most diverse pteridophyte genera (hypotheticals excluded) at La Selva are *Thelypteris, Polypodium*, and *Trichomanes*, which would rank among the ten largest genera of La Selva vascular plants based on data presented by Hammel & Grayum (1982). Table 2 lists the largest genera of pteridophytes at La Selva and at two other neotropical sites for which data are available. Pertinent information regarding all three sites is presented in Table 3; additional data may be found in Croat (1978), Dodson and Gentry (1978), and Hammel (1986). All three sites are in the lowlands, at roughly the same elevation. Barro Colorado Island

TABLE 3. Relevant Abiotic Characteristics and Total Number of Pteridophyte Species for Three Neotropical Sites.

Site	Size (ha)	Elev. (m)	Precip. (mm/yr)	Temp. (°C)	No. spp.
RP[1]	167	150–220	2980[2]	20–28	83[3]
BCI	1560	25–165	2750	21–32	104
LS	1533	37–130	3900	24[4]	173

[1] RP = Río Palenque; BCI = Barro Colorado Island; LS = La Selva.
[2] Datum from Dodson, et al. (1985).
[3] Incorporating updates from A. Gentry (pers. comm.).
[4] Mean annual temperature.

(BCI) in Panama is about the same size as La Selva; however, the Río Palenque reserve in Ecuador is an order of magnitude smaller. Both of the last-named two sites are drier and more seasonal than La Selva, BCI markedly so.

Atwood (1986) judged that "La Selva is most similar generically to Río Palenque" in its orchid flora (as compared with BCI and Volcán Mombacho, Nicaragua); Hammel (1986), on the other hand, found La Selva to "share more genera and species" of six angiosperm families with BCI than with Río Palenque. As regards pteridophytes, La Selva shares the same number of genera (34) with BCI and Río Palenque. Five additional genera (*Botrychium, Anemia, Lygodium, Maxonia,* and *Ceratopteris*) occur at Río Palenque, whereas BCI boasts nine genera not known from La Selva (*Lygodium, Schizaea, Cnemidaria, Acrostichum, Ceratopteris, Maxonia, Triplophyllum, Dictyoxiphium,* and *Salvinia*).

Twenty-eight pteridophyte species are shared among all three of the sites (see Appendix 1). Sixty-five of the 104 pteridophyte species at BCI (about 62.5%) are shared with La Selva, while Río Palenque shares 48 species (57.8% of the total 83). Thirty-seven of the species shared by La Selva and BCI do not occur at Río Palenque. More surprising, perhaps, is the fact that 20 species are shared by La Selva and Río Palenque but do not occur at the geographically intermediate BCI station. Moreover, just four species (*Ceratopteris pteridoides, Asplenium laetum, Maxonia apiifolia,* and *Saccoloma elegans*) are common to BCI and Río Palenque but absent from La Selva.

Similarly ambiguous results are obtained when Sorensen's coefficient of similarity (Sarmiento, 1975) is calculated (at the species level) for these three sites. Comparison of the La Selva and BCI pteridofloras yields the highest figure, 47; the coefficient for La Selva/Río Palenque is 38. However, when Río Palenque is compared with BCI, the value is lower still (32).

We believe that the La Selva pteridoflora is probably more similar to that of Río Palenque, but that this relationship is somewhat obscured by the much smaller size of the latter site and the consequent absence of many species that may occur (or have occurred) in the near vicinity. The latter factor casts a long shadow over absolute-number comparisons among the three sites. La Selva and BCI are comparable in size and elevation, and the fact that La Selva has 65% more pteridophyte species than BCI must be explainable in terms of the significant differ-

ences in amount and distribution of precipitation. Gentry (e.g., 1982) has repeatedly emphasized the importance of precipitation in explaining phytogeographical patterns, and noted that the Río Palenque flora is more like that of Central American wet forests than that of nearby but more seasonal forests in western Ecuador. Lellinger (1975) had previously arrived at essentially the same conclusion regarding the Chocó pteridophyte flora.

Although the total annual precipitation at Río Palenque is not much higher than that at BCI, the effects of the dry season at the former site are somewhat mitigated by prevailing cool and cloudy conditions (A. H. Gentry, pers. comm.). Thus, whereas many seed plant taxa become more predominantly epiphytic in wet forest as opposed to moist forest, these preliminary data suggest that pteridophytes apparently do not. The dramatic increase in epiphytic pteridophytes with increasing elevation, discussed in a later section, is perhaps due to some factor other than absolute precipitation; indeed, the average annual rainfall at the cloud-forest reserve at Monte Verde, Costa Rica, is actually considerably lower than at La Selva (G. S. Hartshorn, pers. comm.).

Growth Habit

The only aspect of growth habit that we investigated was the distribution of epiphytic vs. terrestrial (or epipetric) species. We might have predicted, for example, that the higher diversity of such groups as pteridophytes and Araceae (Grayum, 1982) at La Selva, as compared with BCI, was due to conditions at the former site being more conducive to epiphytes in general on account of the higher precipitation (de la Sota, 1971; Gentry & Dodson, 1987). In fact, epiphytes account for nearly twice as large a percentage of the total vascular flora at La Selva than at BCI (Gentry & Dodson, 1987). Surprisingly, however, the percentage of epiphytic species in the La Selva pteridoflora (41.9%) is not significantly different from that at BCI (40.4%), nor in all probability from that at Río Palenque (35.9%).

Distribution of La Selva Pteridophytes by Habitat

Over half of the 123 spermatophyte species in Hammel's (1986) study occurred in upland primary forest. This is also the favored pteridophyte habitat at La Selva, the corresponding figure being 50.0% (86 species). The most common and characteristic species for each La Selva habitat are listed below, along with the percentage of the total pteridoflora represented there (these figures are not additive, since many fern species occur in two or more habitats).

Upland Primary Forest.—*Danaea wendlandii, Trichomanes collariatum, T. godmanii, Cyathea multiflora, Adiantum obliquum, Asplenium cirrhatum, A. cuspidatum, Elaphoglossum palmense, E. peltatum, Grammitis linearifolia, G. serrulata, Hypolepis hostilis, Lomariopsis fendleri, Polybotrya caudata, P. cervina, Polypodium triseriale, Pteris pungens, Saccoloma inaequale, Salpichlaena volubilis, Thelypteris curta, T. lingulata* (50.0%).

Alluvial Forest.—*Selaginella eurynota, S. flagellata, Adiantum tetraphyllum,*

Dennstaedtia bipinnata, Polypodium percussum, Tectaria nicotianifolia, T. rivalis (26.8%).

Riparian Habitats.—*Selaginella atirrensis, S. umbrosa, Cyathea trichiata, Blechnum occidentale, Tectaria mexicana, Thelypteris angustifolia, T. balbisii, T. francoana, T. torresiana* (21.2%).

Secondary Growth.—*Selaginella arthritica, Alsophila cuspidata, A. firma, Antrophyum lanceolatum, Bolbitis portoricensis, Cyclopeltis semicordata, Dicranoglossum panamense, Diplazium striatastrum, Nephrolepis biserrata, Polypodium aureum, P. ciliatum, P. phyllitidis, P. lycopodioides, Tectaria incisa, Thelypteris nicaraguensis* (19.4%).

Swamp Forest.—*Cyathea ursina, Adiantum tetraphyllum, Diplazium lindbergii, D. macrophyllum, Polypodium occultum, P. sphenodes, Tectaria athyrioides* (13.4%).

Rocky Quebradas.—*Selaginella umbrosa, Trichomanes diaphanum, T. krausii, Asplenium otites, A. repandulum, Bolbitis nicotianifolia, Tectaria plantaginea* (12.3%).

Weedy Areas.—*Adiantum latifolium, A. petiolatum, Hemionitis palmata, Hypolepis repens, Pityrogramma calomelanos, Thelypteris dentata, T. nicaraguensis* (6.7%).

Open Marshes.—*Nephrolepis biserrata, Thelypteris serrata* (1.2%).

Additional data can be found in Appendix 1.

Distribution of La Selva Pteridophytes in Costa Rica

Dogma has it that the pteridoflora of lowland tropical sites is boring and not very diverse, comprising mainly common and widespread lowland species (Wagner & Gómez, 1983). This is not strictly the case at La Selva, which is relatively wet and cool due to its location at the foot of the Central Cordillera. This proximity to the mountains makes La Selva an atypical lowland site when compared to many other parts of the lowland tropics.

Based on data culled from the MO and CR herbaria and summarized by Grayum and Churchill (1988a, b), only 30.1% of the species in the La Selva pteridoflora are restricted (in Costa Rica) to the lowlands (i.e., elevations of less than 1000 m); 10.6% are restricted to elevations of less than 500 m; 55.2% range into mid-elevations (1000–2000 m); and 14.5% to higher elevations (above 2000 m). Six species (*Lycopodium cernuum, Selaginella flagellata, Asplenium cuspidatum, A. serra, Blechnum occidentale,* and *Elaphoglossum peltatum*) ascend to 3000 m or higher.

Only 17.9% of La Selva pteridophyte species are confined, in Costa Rica, to the Caribbean slope (not surprisingly, this total includes nearly 75% of the species restricted to below 500 m).

Since we know of no comprehensive enumeration of pteridophyte species for any mid-elevation (e.g., cloud forest) site in the neotropics, it is difficult to test the hypothesis that such supposedly fern-rich habitats (de la Sota, 1971; Wagner & Gómez, 1983; Lellinger, 1985) are indeed relatively more diverse than La Selva. It seems well established that epiphytes in general are most diverse in mid-

elevation cloud forests (Gentry & Dodson, 1987), where such predominantly epiphytic pteridophyte genera as *Lycopodium*, *Hymenophyllum*, *Blechnum*, *Elaphoglossum*, and *Grammitis* have many species in Costa Rica. Wagner and Gómez (1983) maintain that 70% of the total Costa Rican pteridophyte flora consists of epiphytic species, compared with only 41.9% at La Selva. However, it has also been suggested (Gentry & Dodson, 1987) that this increase in epiphytic species with elevation is countered by a corresponding decrease of terrestrial species. Mainly terrestrial genera such as *Selaginella*, *Danaea*, *Adiantum*, and *Tectaria* are perhaps most diverse in the humid lowlands. *Trichomanes*, though largely epiphytic, has many more terrestrial species in the Costa Rican lowlands than at higher elevations (however, the reverse may be true of other genera, such as *Elaphoglossum*). Tree ferns are often associated with cloud forests; for example, Lee et al. (1987) report that tree-fern diversity in the Monte Verde area is highest in "montane rainforest" (1535–1610 m) and declines at lower elevations. However, the total number of tree-fern species in their entire study area (7) is one less than the La Selva total (including *Metaxya*).

At the country level, it may indeed be true that pteridophytes in general are most diverse at mid-elevations, as is apparently the case in Panama (Lellinger, 1985). Still, it is perhaps of interest in this connection that the estimated percentage of pteridophytes in the La Selva vascular flora (9%) is identical to that in the total Costa Rican flora (9.0%, based on 900 pteridophyte species out of an estimated 10,000 vascular plant species). Dogma also has it that endemism and insularity increase as elevation increases. Thus, we might predict that pteridophyte diversity at a particular mid-elevation site would not necessarily exceed that at La Selva, even given that pteridophytes were more diverse at mid-elevations on the country level. Floristic data from a mid-elevation cloud forest locale such as the Monte Verde reserve in Costa Rica would shed much light on this situation.

Elevation is not, of course, the only factor affecting fern distribution. In a previous section of this paper, the important role of precipitation was alluded to. Other factors are not well understood. For example, Finca El Bejuco, a small biological field station only about 7 km away from La Selva and at approximately the same elevation, harbors numerous pteridophyte species never collected from La Selva (among them *Dicranopteris flexuosa*, *Trichomanes ankersii*, *T. polypodioides*, *T. punctatum*, *T. galeottii*, *Cyathea stolzei*, *Elaphoglossum backhousianum*, *Thelypteris leprieurii*, and *Triplophyllum funestum*; A. R. Smith, in litt.). This is perhaps not very surprising, inasmuch as localized distributions of fern species within the boundaries of La Selva itself have already been discussed. Local climatic or edaphic factors or chance vagaries of dispersal may be responsible for these phenomena.

Biogeographical Affinities of the La Selva Pteridoflora

The following analysis is based on data presented in Grayum and Churchill (1988a, 1988b).

About 83.6% of La Selva pteridophyte species are here considered widespread, that is, having neither their northern nor southern limit of distribution in Costa

Rica. About 7% of these (10 species) are pantropical, occurring also in Asia and/or Africa. Approximately ⅔ of the New World species range into the West Indies, the remainder being strictly continental. Twenty-six (92.9%) of the 28 more narrowly distributed species reach their northern limit in Costa Rica, whereas but two (7.1%) apparently reach their southern limit here (*Pseudocolysis bradeorum* and *Tectaria rufovillosa*).

Not a single La Selva pteridophyte species is known to be endemic to Costa Rica. In contrast, Hammel (1986) reported that about 13% of the angiosperm species in his study "appear to be endemic to Costa Rica." Endemism is in general low in ferns as compared with spermatophytes (Smith, 1972); however, Lellinger (1975) reported 17 endemic species from the Chocó—probably owing to the fact that this region is biogeographically, rather than politically, defined.

Thus, the La Selva pteridoflora comprises mostly very wide-ranging species, yet clearly shows evidence of southern rather than northern affinities. Southern affinities were also evident in the six angiosperm families analyzed by Hammel (1986), who commented that such a relationship "should come as no surprise." This is certainly the case with pteridophytes, especially considering the previously discussed connections between the pteridofloras of Central America and the Chocó region.

Endemism is very low or nonexistent among La Selva pteridophytes, which again probably relates to air-dispersal of fern diaspores.

Phenology

Phenological studies on ferns in general are rare (Wagner & Gómez, 1983), and on La Selva ferns rarer still. Despite their abundance and diversity at La Selva, pteridophytes have been the subject of exceedingly few ecological or demographic studies. Herbarium data suggest that *Selaginella eurynota* is seasonally reproductive, producing strobili mainly from November to January. Ongoing studies by J. Sharpe (pers. comm.) have shown that all five La Selva *Danaea* species exhibit pronounced seasonality in the maturation of their fertile fronds. On the other hand, Moran (1986) suggested that *Olfersia* (*Polybotrya*) *cervina* may be continuously reproductive at La Selva. The La Selva Biological Station is obviously an excellent place for studies of this sort, which would help fill a significant void in our understanding of pteridophyte reproductive biology.

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Literature Cited

Atwood, J. T. 1986. Flora of La Selva, Costa Rica: Orchidaceae. Amer. J. Bot. 73:749.

Correll, D. S. 1956. *Ferns and fern allies of Texas*. Renner, Texas: Texas Research Foundation.

Croat, T. B. 1978. *Flora of Barro Colorado Island*. Stanford: Stanford University Press.

Dodson, C. H. and A. H. Gentry. 1978. Flora of the Río Palenque Science Center. Selbyana 4:1–628.

———, ———, and F. M. Valverde. 1985. *La flora de Jauneche*. Quito: Banco Central de Ecuador.

Edie, H. H. 1978. *Ferns of Hong Kong*. Hong Kong: Hong Kong University Press.

Gentry, A. H. 1982. Phytogeographic patterns as evidence for a Chocó refuge. Pp. 112–135 in *Biological diversification in the tropics*, ed. G. T. Prance. New York: Columbia University Press.

——— and C. H. Dodson. 1987. Diversity and biogeography of neotropical vascular plants. Ann. Missouri Bot. Gard. 74:205–233.

Gómez, L. D. and J. M. Savage. 1983. Searchers on that rich coast: Costa Rican field biology, 1400–1980. Pp. 1–11 in *Costa Rican natural history*, ed. D. H. Janzen. Chicago: University of Chicago Press.

Grayum, M. H. 1982. The aroid flora of Finca La Selva, Costa Rica: a lowland wet forest locality. Aroideana 5:47–59.

——— and H. W. Churchill. 1988a. The vascular flora of La Selva Biological Station, Costa Rica. Lycopodiophyta. Selbyana (in press).

——— and ———. 1988b. The vascular flora of La Selva Biological Station, Costa Rica. Polypodiophyta. Selbyana (in press).

Grillos, S. J. 1966. *Ferns and fern allies of California*. Berkeley: University of California Press.

Hammel, B. E. 1986. Characteristics and phytogeographical analysis of a subset of the flora of La Selva (Costa Rica). Selbyana 9:149–155.

——— and M. H. Grayum. 1982. Preliminary report on the flora of La Selva field station, Costa Rica. Ann. Missouri Bot. Gard. 69:420–425.

Hartshorn, G. S. 1983. Plants: introduction. Pp. 118–183 in *Costa Rican natural history*, ed. D. H. Janzen. Chicago: University of Chicago Press.

Jones, D. L. and S. C. Clemesha. 1981. *Australian ferns and fern allies*. Sydney: A. H. & A. W. Reed.

Kepler, A. K. 1975. *Common ferns of Luquillo Forest, Puerto Rico*. San Juan: Inter American University Press.

Knobloch, I. W. and D. S. Correll. 1962. *Ferns and fern allies of Chihuahua, Mexico*. Renner, Texas: Texas Research Foundation.

Kornaś, J. 1979. *Distribution and ecology of the pteridophytes in Zambia*. Warszawa: Panstwowe Wydawnictwo Naukowe.

Lakela, O. and R. W. Long. 1976. *Ferns of Florida*. Miami: Banyan Books.

Lee, M. A. B., P. A. Burrowes, J. E. Fauth, and J. C. Koella. 1987. The distribution of tree ferns along an altitudinal gradient in Monteverde, Costa Rica. Brenesia (in press).

Lellinger, D. B. 1975. A phytogeographic analysis of Chocó pteridophytes. Fern Gaz. 11:105–114.

———. 1985. The distribution of Panama's pteridophytes. Pp. 43–47 in *The botany and natural history of Panama: La botanica e historia natural de Panamá*, eds. W. G. D'Arcy and M. D. Correa A. Monogr. Syst. Bot. Missouri Bot. Gard. 10:1–455.

Mickel, J. T. 1967. An advanced course in pteridophyte biology in Costa Rica. Amer. Fern J. 57: 145–161.

Moran, R. C. 1986. The neotropical fern genus *Olfersia*. Amer. Fern J. 76:161–178.

OTS (Organization for Tropical Studies). 1967. *Biology of tropical pteridophytes*. Unpublished bound volume, OTS library, San Pedro de Montes de Oca, Costa Rica.

Proctor, G. R. 1985. *Ferns of Jamaica*. London: British Museum (Natural History).

Sarmiento, G. 1975. The dry plant formations of South America and their floristic connections. J. Biogeog. 2:233–251.

Smith, A. R. 1972. Comparison of fern and flowering plant distributions with some evolutionary interpretations for ferns. Biotropica 4:4–9.

———. 1981. Pteridophytes. Pp. 1–370 in *Flora of Chiapas, Part 2*, ed. D. E. Breedlove. San Francisco: California Academy of Sciences.

SOTA, E. DE LA. 1971. El epifitismo y las Pteridofitas en Costa Rica. Nova Hedwigia 21:401–465.

TRYON, R. M. and A. F. TRYON. 1968. Edith Scamman (1882–1967). Amer. Fern J. 58:1–4.

WAGNER, W. H. and L. D. GÓMEZ. 1983. Pteridophytes (helechos, ferns). Pp. 311–318 in *Costa Rican natural history*, ed. D. H. Janzen. Chicago: University of Chicago Press.

WILBUR, R. L. 1986. The vascular flora of La Selva Biological Station, Costa Rica. Introduction. Selbyana 9:191.

APPENDIX 1. CHECKLIST OF THE PTERIDOPHYTES OF LA SELVA

Species	Habit	Habitat	Abundance	Distr.
	Division Lycopodiophyta			
	Family Selaginellaceae			
Selaginella anceps C. Presl	TEl	A	3	
Selaginella arthritica Alston	Tl	SAd	4	BCI
Selaginella atirrensis Hieron.	Tl	R	4	
Selaginella bombycina Spring	Ee	Q	2	
Selaginella eurynota A. Braun	TLl	AdW	4	
Selaginella flagellata Spring	TLEUl	Ad	4	BCI
Selaginella oaxacana Spring	Tl	AZ	3	
Selaginella silvestris Aspl.	Tl	Ad	1	RP
Selaginella umbrosa Lemaire ex Hieron.	ELTl	RQ	4	
	Family Lycopodiaceae			
Lycopodium cernuum L.	Tl	Rd	1	BCI
Lycopodium dichaeoides Maxon	Ce	P	1	
Lycopodium dichotomum Jacq.	Ce	PA	2	BCI
Lycopodium linifolium L.	CUe	ASPw	3	RP
	Division Polypodiophyta			
	Family Ophioglossaceae			
Ophioglossum reticulatum L.	Te	W	1	BCI
	Family Marattiaceae			
Danaea cuspidata Liebm.	Te	P	1	
Danaea elliptica J. E. Smith	Te	Pr	2	
Danaea grandifolia L. Underw.	Te	PwrZ	1	
Danaea nodosa (L.) J. E. Smith	Te	Pw	3	BCI
Danaea wendlandii Reichb. f.	Te	P	4	
	Gleicheniaceae			
Dicranopteris pectinata (Willd.) L. Underw.	Tl	R	(1)	BCI, RP
Gleichenia bifida (Willd.) Spring	Tl	Rd	2	
	Hymenophyllaceae			
Hymenophyllum brevifrons Kunze	Cl	P	1	BCI
Hymenophyllum hirsutum (L.) Sw.	ULl	P	2	
Hymenophyllum maxonii Christ ex Morton	Ul	P	3	
Hymenophyllum polyanthos (Sw.) Sw.	UCLl	P	3	
Trichomanes angustifrons (Fée) W. Boer	Ul	PA	2	
Trichomanes ankersii Parker ex Hook. & Grev.	Ul	Pr	(1)	
Trichomanes collariatum Bosch	Hl	P	4	RP
Trichomanes crispum L.	Ce	P	1	

APPENDIX 1. CONTINUED

Species	Habit	Habitat	Abundance	Distr.
Trichomanes curtii Rosenstock	Ul	P	1	
Trichomanes diaphanum H.B.K.	UEl	QPw	3	
Trichomanes diversifrons (Bory) Mett.	Te	PrA	2	BCI
Trichomanes ekmanii W. Boer	Ul	P	2	BCI
Trichomanes elegans Rich.	Te	Pw	2	
Trichomanes godmanii Hook.	Ul	P	4	BCI
Trichomanes krausii Hook. & Grev.	UEl	QS	3	BCI, RP
Trichomanes membranaceum L.	UEl	Pw	3	RP
Trichomanes osmundoides DC.	Te	R	(1)	
Trichomanes pinnatum Hedwig	Te	Pr	1	BCI
Trichomanes rigidum Sw.	Te	P	1	
Trichomanes tuerckheimii Christ	Ul	Pr	1	
Metaxyaceae				
Metaxya rostrata (H.B.K.) C. Presl	Ts	Pr	1	BCI
Cyatheaceae				
Alsophila cuspidata (Kunze) Conant	Ta	SP	4	BCI, RP
Alsophila firma (Baker) Conant	Ta	S	4	
Cyathea microdonta (Desv.) Domin	Ta	RdS	2	BCI
Cyathea multiflora J. E. Smith	Ta	Pw	4	
Cyathea schiedeana (C. Presl) Domin	Ta	Z	1	
Cyathea trichiata (Maxon) Domin	Ta	R	3	BCI, RP
Cyathea ursina (Maxon) Lellinger	Te	Z	2	
Polypodiaceae				
Adiantum latifolium Lam.	Tl	WRdPw	4	RP
Adiantum macrophyllum Sw.	Ts	R	2	RP
Adiantum obliquum Willd.	Tsl	Pd	4	BCI
Adiantum petiolatum Desv.	Tls	WRd	4	BCI, RP
Adiantum seemannii Hook.	Ts	R	1	BCI
Adiantum tetraphyllum H. & B. ex Willd.	Tsl	ZA	3	BCI, RP
Adiantum wilsonii Hook.	Tl	R	1	
Anetium citrifolium (L.) Splitg.	Ul	PZ	3	BCI, RP
Antrophyum cajenense (Desv.) Spreng.	Us	P	2	
Antrophyum lanceolatum (L.) Kaulf.	Us	SP	3	
Antrophyum lineatum (Sw.) Kaulf.	Us	P	*	
Asplenium abscissum Willd.	Ee	Q	1	
Asplenium cirrhatum Rich. ex Willd.	LEe	P	3	
Asplenium cuspidatum Lam.	CUe	PSA	4	BCI
Asplenium falcinellum Maxon	UCe	P	3	BCI
Asplenium formosum Willd.	LEe	R	2	
Asplenium holophlebium Baker	Ul	Pw	2	
Asplenium otites Link	Ee	Q	2	
Asplenium pteropus Kaulf.	Ue	Pw	1	BCI, RP
Asplenium repandulum Kunze	Es	Q	3	
Asplenium serra Langsd. & Fisch.	UCs	P	3	
Asplenium serratum L.	UCe	P	3	BCI, RP
Blechnum fraxineum Willd.	Te	R	1	
Blechnum occidentale L.	Te	Rd	3	
Blechnum polypodioides Raddi	Te	Pd	1	

Appendix 1. Continued

Species	Habit	Habitat	Abundance	Distr.
Bolbitis aliena (Sw.) Alston	TEs	QPw	1	
Bolbitis nicotianifolia (Sw.) Alston	Es	Q	3	BCI, RP
Bolbitis nicotianifolia (Sw.) Alston	Hl	PwZ	2	
Bolbitis portoricensis (Sprengel) Hennipman	TEs	QSA	3	BCI
Ctenitis sloanei (Poeppig ex Sprengel) Morton	TLe	RAd	1	BCI
Ctenitis subincisa (Willd.) Ching	Te	SAw	2	RP
Cyclopeltis semicordata (Sw.) J. Smith	Te	S	4	BCI, RP
Dennstaedtia bipinnata (Cav.) Maxon	Tl	AdS	3	
Dennstaedtia cicutaria (Sw.) T. Moore	Tl	R	2	BCI, RP
Dennstaedtia obtusifolia (Willd.) T. Moore	Ts	Pw	2	RP
Dicranoglossum panamense (C. Chr.) L. D. Gómez	Ue	SA	3	BCI
Didymochlaena truncatula (Sw.) J. Smith	Te	Aw	3	RP
Diplazium cristatum (Desr.) Alston	Te	Aw	1	RP
Diplazium grandifolium (Sw.) Sw.	Te	R	1	BCI
Diplazium ingens Christ	Te	Z	1	
Diplazium lindbergii (Mett.) Christ	Te	Z	3	
Diplazium lonchophyllum Kunze	Te	R	2	
Diplazium macrophyllum Desv.	Te	ZPw	3	
Diplazium pactile Lellinger	Te	Z	2	
Diplazium striatastrum Lellinger	Ta	SAZ	4	RP
Elaphoglossum amygdalifolium (Mett.) Christ	Ul	Aw	2	RP
Elaphoglossum herminieri (Bory ex Fée) T. Moore	Cs	P	3	BCI, RP
Elaphoglossum latifolium (Sw.) J. Smith	Cs	P	3	
Elaphoglossum palmense Christ	CUs	P	4	
Elaphoglossum peltatum (Sw.) Urban	Cl	P	3	
Elaphoglossum sp. nov., ined.	Us	Pw	3	
Grammitis linearifolia (Desv.) Steudel	Ce	PA	4	
Grammitis serrulata (Sw.) Sw.	CLl	PA	3	
Grammitis turrialbae (Christ) Seymour	Us	P	*	
Hecistopteris pumila (Sprengel) J. Smith	CLl	P	2	
Hemidictyum marginatum (L.) C. Presl	Te	R	1	BCI, RP
Hemionitis palmata L.	TLe	WAd	4	
Hypolepis hostilis (Kunze) C. Presl	Tl	Pd	4	
Hypolepis repens C. Presl	Tl	WAd	4	
Lastreopsis exculta (Mett.) Tindale subsp. *guatemalensis* (Baker) Tindale	Ts	R	3	
Lindsaea lancea (L.) Bedd. var. *lancea*	Ts	Pr	1	
Lindsaea quadrangularis Raddi subsp. *subalata* Kramer	Ls	Prw	1	
Lomariopsis fendleri D. Eaton	Hl	P	4	BCI
Lomariopsis japurensis (Martius) J. Smith	Hl	SAd	3	RP
Lonchitis hirsuta L.	Tes	RAwSw	3	
Nephrolepis biserrata (Sw.) Schott	TULe	SWZMPd	4	BCI
Nephrolepis multiflora (Roxb.) Jarrett ex Morton	TUe	S	2	
Nephrolepis pendula (Raddi) J. Smith	Ue	A	3	BCI, RP
Nephrolepis rivularis (Vahl) Mett. ex Krug	UCe	P	2	
Oleandra articulata (Sw.) C. Presl	ULCl	P	2	
Pityrogramma calomelanos (L.) Link	Te	WRd	3	BCI, RP
Pityrogramma tartarea (Cav.) Maxon	Te	Rd	(1)	

APPENDIX 1. CONTINUED

Species	Habit	Habitat	Abundance	Distr.
Polybotrya alfredii Brade	HUl	P	1	
Polybotrya caudata Kunze	Hl	P	4	BCI
Polybotrya cervina (L.) Kaulf.	LTs	Pd	4	
Polybotrya osmundacea H. & B. ex Willd.	HTl	ZP	3	RP
Polypodium angustifolium Sw.	Cs	Z	2	RP
Polypodium aureum L.	UCs	SP	3	
Polypodium ciliatum Willd.	CUl	SA	4	BCI, RP
Polypodium crassifolium L.	Us	RZQ	2	BCI
Polypodium dissimile L.	Us	SAQ	3	
Polypodium furfuraceum Schlecht. & Cham.	Cs	PA	3	
Polypodium hygrometricum Splitg.	UEl	SR	2	BCI
Polypodium loriciforme Rosenstock	UCl	PS	4	
Polypodium lycopodioides L.	Cl	SPA	4	BCI
Polypodium maritimum Hieron.	Cl	AP	3	BCI, RP
Polypodium occultum Christ	Us	ZA	2	BCI
Polypodium pectinatum L.	UCs	AS	3	BCI
Polypodium percussum Cav.	CUl	AP	4	BCI, RP
Polypodium phyllitidis L.	Us	SA	4	
Polypodium sororium H. & B. ex Willd.	Ul	P	3	
Polypodium sphenodes Kunze ex Klotzsch	Ul	ZQP	2	
Polypodium triseriale Sw.	Cl	P	3	BCI
Pseudocolysis bradeorum (Rosenstock) L. D. Gómez	Ul	QSZR	2	
Pteris altissima Poiret	Tes	ZAws	3	BCI, RP
Pteris propinqua Agardh	Te	AdW	2	BCI
Pteris pungens Willd.	Te	P	3	BCI
Pteris quadriaurita Retz.	Te	Rd	(1)	
Saccoloma inaequale (Kunze) Mett.	Te	Pd	4	
Salpichlaena volubilis (Kaulf.) J. Smith	Tv	P	4	
Stigmatopteris longicaudata (Liebm.) C. Chr.	Te	Q	1	
Stigmatopteris nephrodioides (Klotzsch) C. Chr.	Te	Z	1	
Tectaria athyrioides (Baker) C. Chr.	Tes	Z	3	
Tectaria brauniana (Karsten) C. Chr.	Ts	Pw	2	
Tectaria draconoptera (D. Eaton) Copel.	Te	Pw	3	
Tectaria incisa Cav.	TEe	SAwQR	4	BCI, RP
Tectaria mexicana (Fée) Morton	TEs	RAd	4	
Tectaria nicotianifolia (Baker) C. Chr.	Tl	AS	3	BCI, RP
Tectaria plantaginea (Jacq.) Maxon	Es	Q	2	
Tectaria rivalis (Mett. ex Kuhn) C. Chr.	Te	A	2	
Tectaria rufovillosa (Rosenstock) C. Chr.	Te	P	1	
Thelypteris angustifolia (Willd.) Proctor	TLs	R	2	RP
Thelypteris balbisii (Sprengel) Ching	TLe	R	4	BCI
Thelypteris biolleyi (Christ) Proctor	Te	S	2	
Thelypteris curta (Christ) Reed	Te	A	3	
Thelypteris decussata (L.) Proctor	Te	Pdw	2	
Thelypteris dentata (Forssk.) E. St. John	TLs	WQ	4	BCI, RP
Thelypteris falcata (Liebm.) R. Tryon	TLs	PwS	2	
Thelypteris francoana (Fourn.) Morton	TLe	R	3	RP
Thelypteris ghiesbreghtii (Hook.) Morton	Tl	S	3	
Thelypteris gigantea (Mett.) Morton	TLEs	QZ	1	RP

APPENDIX 1. CONTINUED

Species	Habit	Habitat	Abundance	Distr.
Thelypteris hispidula (Decne.) Reed	Te	S	2	
Thelypteris leprieurii (Hook.) R. Tryon	TEe	R	(1)	
Thelypteris lingulata (C. Chr.) Morton	Ts	P	4	
Thelypteris nicaraguensis (Fourn.) Morton	TLEe	SQW	4	BCI
Thelypteris poiteana (Bory) Proctor	Tl	W	2	BCI, RP
Thelypteris resinifera (Desv.) Proctor	Te	R	1	RP
Thelypteris serrata (Cav.) Alston	TLs	RMQ	2	BCI
Thelypteris torresiana (Gaud.) Alston	Ts	RAd	4	BCI, RP
Thelypteris urbanii (Sodiro) A. R. Smith	Te	Aw	2	
Thelypteris villana L. D. Gómez	ETe	Q	(1)	
Vittaria costata Kunze	Us	SP	2	BCI
Vittaria lineata (L.) J. E. Smith	CUEe	AP	3	BCI
Vittaria stipitata Kunze	CUe	PA	3	

LEGEND FOR APPENDIX 1

Habit.—Two types of information are encoded here: the substrate is indicated by a capital letter, and the nature of the rhizome by a lower-case letter.

C—Canopy epiphytes; sometimes found closer to the ground, as in light gaps or pejibaye trunks; may be frequently encountered on branchfalls.

E—Epipetric; growing on rocks or, occasionally, concrete.

H—Hemiepiphytes; species which begin life on the ground, or very close to it, and at maturity are characteristically appressed-climbers on trunk bases (the connection with the ground commonly being lost).

L—Log-dwellers; species that are typically found growing on rotting logs or, occasionally, timber (epiphytes may persist on fallen trees for some time, and many terrestrial species are occasionally seen on logs as well).

T—Terrestrial species.

U—Understory epiphytes; including mainly trunk epiphytes, having no close association with the ground.

a—arborescent; species with a distinct, self-supporting trunk of at least 0.5 m in height.

e—erect; species with a short, erect rhizome, the fronds closely approximate in a rosette (most terrestrial ferns fit this description).

l—long-creeping rhizome, the fronds arising rather distantly.

s—short-creeping rhizome, the fronds more or less approximate and often clustered at the apex.

v—vining; ferns with an erect rhizome, climbing high into adjacent foliage by means of the greatly elongated frond axes (at La Selva, only a single species falls into this category).

For either of the two subcategories of "Habit" (as well as for the "Habitat" subcategories) two or more alternative conditions may be indicated for a given species. These are always listed in order of prevalence: thus, "CUe" describes a species with erect rhizome which is predominantly a canopy epiphyte, but sometimes occurs in the understory; similarly, "Tls" would be used to characterize a terrestrial species with rhizomes that are long-creeping, or sometimes short-creeping.

Habitat.—This category regularly has one component, and sometimes a second. The broad habitat preference is always indicated by a capital letter. A microhabitat within that habitat may be specified by the use of an appropriate lower-case letter.

A—Alluvial forest; forest which exists on alluvial soils, especially along the major rivers and in the vicinity of the Quebrada (Q.) Leonel, and near the lower reaches of the Q. El Salto, Q. El Surá (including the Arboretum) and Q. Sábalo.

M—Marshes; open, treeless, wet sites (a very poor fern habitat at La Selva).
P—Primary forest; comparatively well-drained slopes and plateaus in upland primary forest, the habitat that prevails over most of La Selva.
Q—Quebradas; small, usually rocky, fast-moving streams, and similar sections of larger streams (e.g., the Q. Esquina, and the Q. El Salto beyond line 2800).
R—Riparian; the banks of the larger rivers, as well as the lower portions of the Q. El Salto, Q. Sábalo and Q. El Surá.
S—Secondary forest; includes abandoned cacao plantations and formerly cleared land in various stages of regeneration. Since much of this habitat at old La Selva occurs in areas of former alluvial forest, the two subcategories are not always clearly defined.
W—Weedy land; regularly maintained or recently abandoned clearings, groves, pastures, etc. The pejibaye grove, the station clearing and first-year successional strips are good examples.
Z—Swamp forest; forested swampy areas, as exemplified by most of Plot II; many of the species of this habitat also occur along sluggish sections of streams.
d—disturbed areas, such as light gaps, landslides or trailsides.
r—ridges or hilltops, generally toward the back of the property.
w—wet or damp, low-lying sites, often near streams or marshes, or on seeps.

Abundance.—The estimates of abundance are relevant only within the context of the habitat of the fern under consideration.

1—very rare; known from only 1–2 collections. The casual observer should not expect to encounter any of these.
2—rare; known from 3–5 collections. The casual observer might expect to encounter some of the species in this category, but no given one.
3—occasional; widely scattered but nowhere common, or else locally abundant. The casual observer has a good chance of seeing any of these.
4—abundant; the casual observer, in the right habitat, will be hard-pressed to overlook these species.
( )—hypothetical; species not known from La Selva proper, but collected in immediately adjacent areas–usually the "Cloud Forest Ridge," or along the Río Peje.
* —dubious; species indicated for La Selva by properly identified collections believed to incorporate label errors as to locality.

Distribution.

BCI—species shared with Barro Colorado Island, Panama.
RP —species shared with the Río Palenque Science Center, Ecuador.

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The Disposition of *Trichopteris* (Cyatheaceae)

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The delimitation of genera and families has been a persistent problem in fern taxonomy, and the Cyatheaceae *sensu stricto* is no exception. Christensen (1905–06) adopted clearly artificial genera (*Cyathea*, *Hemitelia*, and *Alsophila*) based on complete (totally surrounding the sorus), partial, and absent indusia. He included *Lophosoria* and *Metaxya* in *Alsophila*. The latter two satellite genera are only distantly related to the major genera of the family, and nowadays are often placed in one or two families of their own.

Holttum (1963) proposed a single genus *Cyathea* for the Flora Malesiana region with two very distinct subgenera, *Sphaeropteris* and *Cyathea*. Holttum has maintained (1981, p. 466) that the "only subdivision of the genus clearly definable is that between subgenus *Sphaeropteris* and the rest." This indicates that *Alsophila* and *Cnemidaria* are less distinct from *Cyathea* than all three are from *Sphaeropteris*, which is confirmed by the lack of hybrids with *Sphaeropteris*. In studying the species of the Flora Malesiana region, Holttum came to the fundamental conclusion, among many, that indusium type is not an important generic character, for within a few species it varies widely.

Tryon (1970) divided the Cyatheaceae *sensu stricto* on the basis of scale characters, indusium presence or absence, and venation. He adopted the genera *Sphaeropteris* (scales conform), *Alsophila* and *Nephelea* (scales non-conform and setate), *Trichopteris* (scales non-conform and non-setate, laminae free-veined, and sori exindusiate), *Cyathea* (scales non-conform and non-setate, laminae free-veined, and sori indusiate), and *Cnemidaria* (scales non-conform and non-setate and laminae net-veined. According to Holttum and Edwards (1983, p. 179), this classification has assorted closely related species into *Cyathea*, *Sphaeropteris*, and *Trichopteris*. It is apparent that genera based on these characters are not natural.

Working from Tryon's (1970) generic concepts, I have found it possible to define readily recognizable and coherent genera in the Cyatheaceae *sensu stricto* by including in *Cyathea* the genus *Trichopteris* and the New World species considered to be *Sphaeropteris*, except for the *S. horrida* group. I accept the genera *Sphaeropteris*, *Alsophila* (including *Nephelea*), *Cyathea* (including *Trichopteris*), and *Cnemidaria*.

Occasional hybrids occur within *Alsophila* and *Cyathea* and between *Cnemidaria* and *Cyathea*. This is evidence of a greater degree of relationship than with *Sphaeropteris*, but in my opinion should not alone be the basis for adopting an inclusive *Cyathea* (either excluding or even including *Sphaeropteris*), for the characteristics of *Alsophila* and *Cnemidaria* are sufficiently different from those of *Cyathea* to distinguish the genera readily, and intergeneric hybrids in ferns are by no means rare and sometimes occur between large and supposedly separate genera (e.g., *Dryopteris* × *Polystichum*).

Sphaeropteris is almost entirely an Old World genus. Only *S. horrida* (Liebm.) Tryon and five allied species occur in the New World tropics. I agree with Holttum and Edwards (1983, pp. 161–162) in this delimitation. The other New World species that were placed in *Sphaeropteris* belong to *Cyathea*. In its restricted sense, this group was monographed by Tryon (1971). The stipe base scales of *Sphaeropteris* are distinct from those of all other New World Cyatheaceae genera in having cells of the same thickness and color from the central portion of the scales to the margin, except for some spreading, spinelike, often darker setae along the margins. The spores of *Sphaeropteris* bear flattened projections that are unique among New World Cyatheaceae (Gastony & Tryon, 1976). The laminae of *Sphaeropteris* are mostly 2-pinnate-pinnatifid (as in most *Cyathea* species), the pinnule segments are often falcate, and the abaxial surface is often pale and bears whitish scales on the abaxial surface. The scales of *Cyathea poeppigii* (Hook.) Domin [syn. *Sphaeropteris elongata* (Hook.) Tryon] and *C. myosuroides* (Liebm.) Tryon mimic those of *Sphaeropteris*, but are subtly different in their marginal body cells and setae (see key couplet 1).

Alsophila has over 200 species in the Old World and 30 (plus several hybrids) in the New World tropics. The New World species were monographed by Conant (1983), who correctly, in my opinion, included in the genus those species that had previously been monographed under the generic name *Nephelea* by Gastony (1973). The cells of the main body of the stipe base scales in *Alsophila* are not at all uniform, and at least an apical, spinelike seta, usually dark in color, is present; many species also have such setae along the lateral margins of the scales. The laminae are 2-pinnate-pinnatifid or more dissected and are often dark green; in some species the axes of the laminae are purplish-black.

Cyathea is the largest genus in the family. Many species occur in the Old World, and I count about 116 species in the New World. As I delimit the genus, it includes many species that have been placed in *Sphaeropteris* and *Trichopteris* by Tryon (1970). The species of *Cyathea* are treated by Tryon (1976), Windisch (1977, 1978), and Barrington (1978) under the aforementioned names. Most of the New World species have 2-pinnate-pinnatifid laminae; others (including a few diminutive species or depauperate specimens) are less divided, even merely pinnate-pinnatifid or pinnate. The sinuses between the segments or lobes are narrow and U-shaped, unlike those of many *Cnemidaria* species. The stipe base scales are concolorous or weakly to rather strongly bicolorous and lack marginal spinelike setae, and so differ from those of *Alsophila* and *Sphaeropteris*. They may have straight marginal cells and scales with entire margins, contorted marginal cells and scales with erose margins, elongate marginal cells and scales with fringelike margins, or, in a few cases, scales bearing marginal spinelike processes (see key couplet 1). The structure of these scales is a valuable character in assessing the relationship of species within the genus. The indusia vary from membranaceous and complete (sphaeropteroid) to firm and saucer-shaped (cyatheoid) to scalelike (hemitelioid) to absent.

Cnemidaria is an exclusively New World tropical genus that includes 25 species. It was monographed by Stolze (1974). The species of *Cnemidaria* have low, erect caudices and lack the tall, treelike trunks typically found in the other genera.

The veins are regularly anastomosing or nearly so, as stated in the key. The laminae are only pinnate-pinnatifid, with relatively low lobes or segments that have large, open, V-shaped sinuses between them. The abaxial surface of the laminae and its axes tend to be glabrous or nearly so with little variety in indument, unlike the foregoing genera. The spores are distinctive in being smooth (Stolze, pers. comm.) and in having three equatorial pores.

The species that have been placed in *Trichopteris* belong to several evolutionary lines and appear to be related to different species or species groups in *Cyathea*.

Cyathea atrovirens (Langsd. & Fisch.) Domin and *C. dichromatolepis* (Fée) Domin appear to have given rise to the series *C. miersii* (Hook.) Domin, *C. elegantula* Domin, and *C. corcovadensis* (Raddi) Domin, the type of the generic name *Trichopteris*. All have similar stipe base scales with contorted marginal cells and bullate and plane scales on the abaxial costae or costules. However, *C. corcovadensis* has the least lobed pinnae or pinnules and the fewest hairs on the adaxial surface of the costae and costules, a common correlation in "*Trichopteris*."

Cyathea sipapoensis (Tryon) Lellinger and *C. marginalis* (Klotzsch) Domin appear to be related to *C. macrocarpa* (Presl) Domin. All have similar stipe base scales that are concolorous, whitish, and with little cellular differentiation.

Two groups of "*Trichopteris*" species share rather strongly bicolorous rhizome scales with an elaborated, fringe-like margin. Almost all of these have conform apices, although not all have the apices articulate, another common correlation in "*Trichopteris*." I have not found likely ancestral species elsewhere in *Cyathea* for these groups, which may indicate their relative remoteness within the genus. In the pinnate group, *C. speciosa* Willd. appears to be least specialized and more like other species of *Cyathea* in having non-conform lamina apices; the related species are *C. cyclodium* (Tryon) Lellinger, *C. stolzei* A. R. Smith ex Lellinger, and *C. williamsii* (Maxon) Domin. All are subarborescent. In the bipinnate group, *C. petiolata* (Hook.) Tryon may be least specialized because it has non-conform apices and is clearly arborescent (caudices to 5 m); *C. conformis* (Tryon) Stolze and *C. intramarginalis* (Windisch) Lellinger also are arborescent, but have conform lamina apices. The remaining species are all subarborescent, with caudices usually less than 1 m long. *Cyathea intramarginalis* is related to *C. dissimilis* (Morton) Stolze; both share the character of l-forked veins, a reduction from the usual pinnate branching of the vein groups that terminates in *C. akawaiorum* Edwards, which has mostly simple veins. The other species of this group are *C. impar* Tryon and *C. steyermarkii* Tryon.

Key to the Genera of Neotropical Cyatheaceae *sensu stricto*

1. Cells of the stipe scales entirely uniform (the marginal and apical spinelike processes excepted), the cells along the margin not different from the central ones; spinelike processes present at the apex and margins of the stipe scales, these regular, antrorse, usually distant, and often dark; basal basiscopic vein of each vein group always arising from the costa; spores

bearing flattened, scalelike projections; indusia sphaeropteroid ..... *Sphaeropteris*

1. Cells of the stipe scales not entirely uniform, the cells along the margins slightly to markedly different in size, shape, wall thickness, or orientation from the central ones; spinelike processes absent (except in *Alsophila*, with strongly bicolorous scales and in *Cyathea poeppigii*, *myosuroides*, and *senilis*, with thinner-walled scales along the margins and irregular, often spreading, usually approximate spinelike processes), but approximate, thin, long, filamentous processes present in some species of *Cyathea*; basal basiscopic vein of each vein group not arising from the costa; spores bearing hairlike projections, granular deposits, or ridges, or nearly smooth; indusia cyatheoid, hemitelioid, sphaeropteroid, or absent.
2. Stipe scales provided with a dark (rarely pale) apical seta and sometimes lateral setae, the scales strongly bicolorous, the central band often several cells thick at the base; peripore of spores ridged ... *Alsophila*
2. Stipe scales lacking apical or lateral spinelike processes (approximate or rarely distant, lateral, rather thin setalike processes at entirely right angles to the axis of the scale present in a few species of *Cyathea*, especially in the *C. swartziana* group), the scales concolorous to weakly bicolorous, the central band usually only 1 cell thick at the base, the apex filamentous to round; perispore of spores not ridged.
3. Basal veins of each vein group forming regular areolae along the costae or the basal veins connivent to the base of the sinus or occasionally meeting the sinus just above the base; plants not arborescent; spores nearly smooth, bearing a single pore at or near the equator on each of the 3 sides; laminae mostly pinnate-pinnatifid with shallowly lobed pinnae and the sinuses between the lobes broadly V-shaped ..... *Cnemidaria*
3. Basal veins usually free and not connivent or anastomosing (except a transverse costal vein joining adjacent pinnate vein groups in *C. petiolata* and *williamsii*); plants arborescent or sometimes subarborescent; spores lacking equatorial pores; laminae mostly 2-pinnate-pinnatifid with deeply lobed pinnules and the sinuses between the lobes narrowly U-shaped ..... *Cyathea*

All of the species of the New World that had been placed in *Sphaeropteris* and most that had been placed in *Trichopteris* have valid names in *Cyathea*. For the few that do not, I wish to make the following combinations:

9910 **Cyathea axillaris** (Fée) Lellinger, comb. nov.—*Phegopteris axillaris* Fée, Gen. 9909 Fil. 243. 1852, effectively a nom. nov. based on *Polypodium axillare* Raddi, 1819, non Aiton, 1789. 21083

9913 **Cyathea barringtonii** A. R. Smith ex Lellinger, nom. nov.—*Alsophila cordata* Klotzsch, Linnaea 20:441. 1847, non *Cyathea cordata* (Desv.) Mett. ex Diels in Engl. & Prantl, 1899.

9915 **Cyathea cyclodium** (Tryon) Lellinger, comb. nov.—*Trichopteris cyclodium* Tryon, Rhodora 74:446. 1972.

Cyathea demissa (Morton) A. R. Smith ex Lellinger, comb. nov.—*Alsophila demissa* Morton, Fieldiana, Bot. 28(1):7. 1955.

Cyathea dombeyi (Desv.) Lellinger, comb. nov.—*Alsophila dombeyi* Desv. Mém. Soc. Linn. Paris 6:320. 1827.

Cyathea gardneri (Hook.) Lellinger, comb. nov.—*Alsophila gardneri* Hook. Sp. Fil. 1:40. 1844.

Cyathea nanna (Barrington) Lellinger, comb. nov.—*Trichopteris nanna* Barrington, Rhodora 78:3, t. 1, f. 3, 4. 1976.

Cyathea pauciflora (Kuhn) Lellinger, comb. nov.—*Alsophila pauciflora* Kuhn, Linnaea 36:156. 1869.

Cyathea rufa (Fée) Lellinger, comb. nov.—*Alsophila rufa* Fée, Crypt. Vasc. Brés. 1:165. 1869.

Cyathea tryonorum (Riba) Lellinger, comb. nov.—*Alsophila tryonorum* Riba, Rhodora 69:66. 1967.

Cyathea venezuelensis A. R. Smith ex Lellinger, nom. nov.—*Trichopteris steyermarkii* Tryon, Rhodora 74:446, f. 11, 12. 1972, non *Cyathea steyermarkii* Tryon, 1972.

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Literature Cited

Barrington, D. S. 1978. A revision of the genus *Trichipteris*. Contr. Gray Herb. 208:3–93.

Christensen, C. 1905–1906. *Index Filicum*. Copenhagen: Hagerup.

Conant, D. S. 1983. A revision of the genus *Alsophila* (Cyatheaceae) in the Americas. J. Arnold Arbor. 64:333–382.

Gastony, G. J. 1973. A revision of the fern genus *Nephelea*. Contr. Gray Herb. 203:81–148.

———— and R. M. Tryon. 1976. Spore morphology in the Cyatheaceae. II. The genera *Lophosoria*, *Metaxya*, *Sphaeropteris*, *Alsophila*, and *Nephelea*. Amer. J. Bot. 63:738–758.

Holttum, R. E. 1963. Cyatheaceae. Fl. Males. II, 1:65–176.

————. 1981. The tree-ferns of Africa. Kew Bull. 36:463–482, t. 15, 16.

———— and P. J. Edwards. 1983. The tree-ferns of Mt. Roraima and neighbouring areas of the Guayana Highlands with comments on the family Cyatheaceae. Kew Bull. 38:155–188.

Stolze, R. G. 1974. A taxonomic revision of the genus *Cnemidaria* (Cyatheaceae). Fieldiana, Bot. 37:1–98.

Tryon, R. 1970. The classification of the Cyatheaceae. Contr. Gray Herb. 200:3–53.

————. 1971. The American tree ferns allied to *Sphaeropteris horrida*. Rhodora 73:1–19.

————. 1976. A revision of the genus *Cyathea*. Contr. Gray Herb. 206:19–98.

Windisch, P. G. 1977. Synopsis of the genus *Sphaeropteris* (Cyatheaceae) with a revision of the neotropical exindusiate species. Bot. Jahrb. Syst. 98:176–198.

————. 1978. *Sphaeropteris* (Cyatheaceae): The systematics of the group of *Sphaeropteris hirsuta*. Mem. New York Bot. Gard. 29:2–2.

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Germination of *Helminthostachys* Spores

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For nearly a century the spores of the Ophioglossaceae have been sown, but few investigators have succeeded in germinating them (Boullard, 1963). Campbell (1895, 1907) was the most successful in germinating spores of the Ophioglossaceae on soil. He reported the early stages of germination of spores of *Botrychium virginianum* (Campbell, 1895) and of three species of *Ophioglossum* (Campbell, 1907). An earlier report on spore germination in *B. ternatum* by du Buysson (1889) remains in question (Whittier, 1981) because the gametophytes that developed had essentially the same morphology as gametophytes of leptosporangiate ferns.

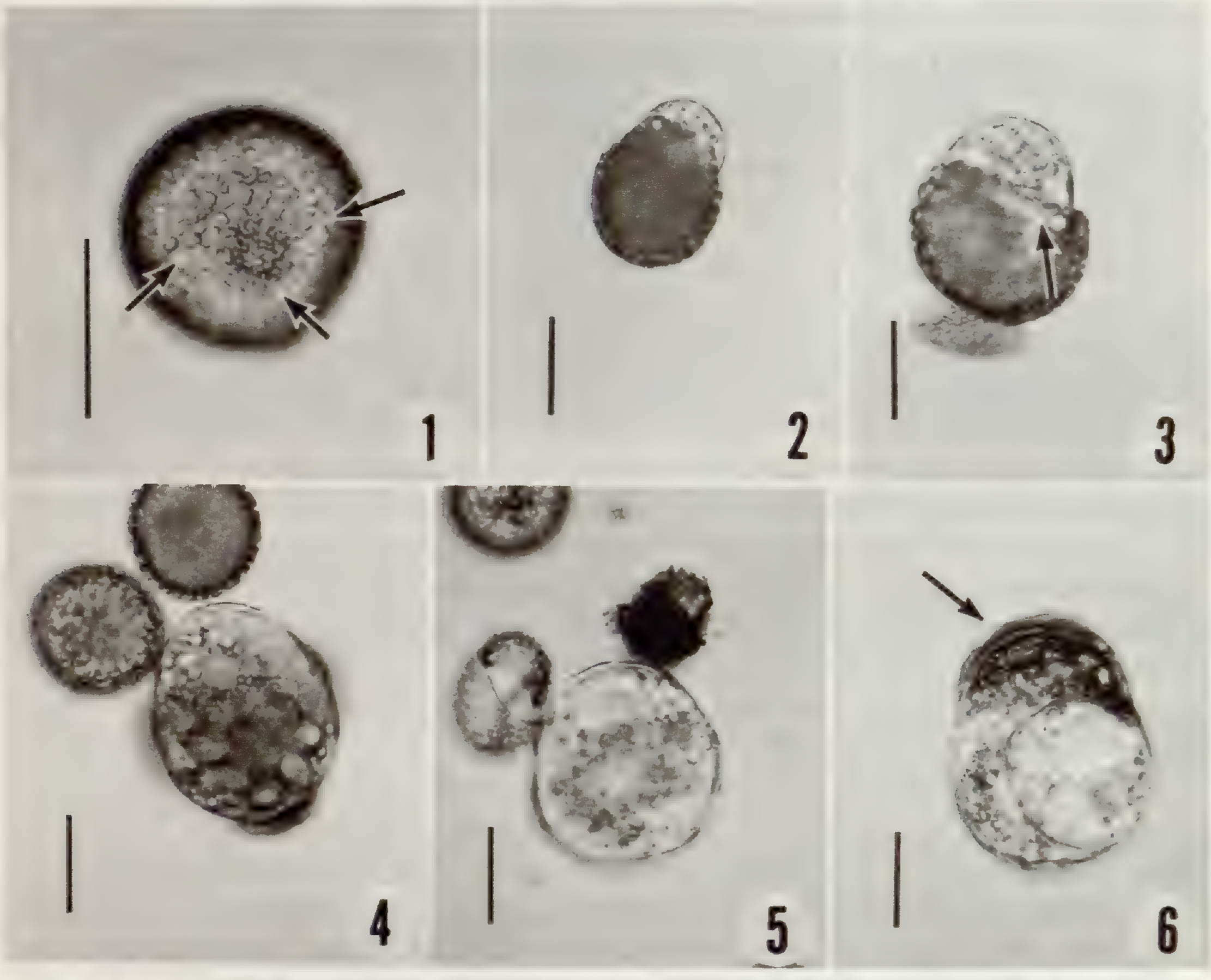
More recently, spores of *Botrychium* and *Ophioglossum* have been germinated in axenic culture (Whittier, 1972, 1981; Gifford & Brandon, 1978). These spores germinated in the dark on nutrient media containing minerals and sugar. In some cases, the spores took 3–4 months to germinate under these conditions (Whittier, 1981).

The mature gametophyte of *Helminthostachys*, the third genus of the Ophioglossaceae, has been described from nature (Lang, 1902; Nozu, 1961; Pant et al., 1984). It usually has a long, thick, cylindrical axis with numerous short lobes at its base. The lobes have apical meristems and appear to be short branches (Pant et al., 1984). The basal region of the gametophyte contains the mycorrhizal fungus and the cylindrical portion bears the gametangia. Spore germination and early stages of gametophyte development are unreported for *Helminthostachys*. Since germination and gametophyte development in *Botrychium* and *Ophioglossum* have been studied with the techniques of axenic culture, the aim of this study was to use these techniques to determine the conditions that promote germination and early gametophyte development in *Helminthostachys*.

MATERIALS AND METHODS

Fertile spikes of *Helminthostachys zeylanica* (L.) Hooker were obtained from plants grown in greenhouses at the New York Botanical Garden, Longwood Gardens, and the University of Massachusetts. The spores were sown within two weeks of their collection from the fertile spikes.

The techniques of Whittier (1973) were employed. Spores were sown on 15 ml of nutrient medium in culture tubes with a diameter of 20 mm. The tubes had screw caps which were tightened to reduce moisture loss. The nutrient medium was composed of a modified Moore's solution of mineral salts, minor elements, FeEDTA, and 0.6% agar. A liter of the modified mineral salt solution contained 100 mg NH_4Cl; 100 mg $MgSO_4 \cdot 7H_2O$; 40 mg $CaCl_2$; and 100 mg K_2HPO_4. The medium was supplemented with 0.2% glucose and had a pH of 5.3 after autoclaving. The spores were cultured at 24 ± 1°C in light at an intensity of 1400 lux from cool white fluorescent lamps or in darkness.



FIGS. 1–6. Germination and early gametophyte development of *Helminthostachys*. All bars = 25 μm. 1. Spore with cristate spore coat. Three arrows indicate ends and point of intersection of two arms of the triradiate ridge. 2. Rupturing of spore coat in early germination. 3. Two-celled gametophyte with spore coat attached. Arrow indicates cell wall separating proximal and distal cells. 4. Two-celled gametophyte with completely ruptured spore coat. 5. Young gametophyte free of spore coat. 6. Three-celled gametophyte with mucilage (arrow) on surface of proximal cell.

RESULTS

The hydrated spores of *Helminthostachys* are almost spherical and have an average diameter of 34 μm. The spore coat is cristate (Fig. 1) which makes observing the contents of the spores difficult. A major portion of the storage materials appears to be lipids since crushing the spores releases large amounts of oil which can be stained with Sudan IV. The triradiate ridge is difficult to observe (Fig. 1) because it is indistinct and small and all surfaces of the spore have the cristate ornamentation. The arms of the triradiate ridge are short with an average length of 10 μm.

After 8 months, spores on the nutrient medium in the dark began to germinate. Spores that were kept on the nutrient medium in the light for over a year failed to germinate.

Rupturing of the triradiate ridge initiates germination. The spore cracks open and the enlarging cell protrudes. This original protrusion has a small diameter

initially (Fig. 2) because of the small-sized triradiate ridge. The ornamented spore coat hinders observation of the first cell division in the enlarging cell. However, as the protrusion enlarges, a cell wall can be seen at the base of the protrusion (Fig. 3). The first division of the enlarging cell is perpendicular to the polar axis of the spore. This division produces a proximal cell (near the triradiate ridge), the protruding cell, and a distal cell (away from the triradiate ridge), which initially remains inside the spore coat.

The enlarging two-celled gametophyte, especially the distal cell, ruptures the spore coat more completely (Figs. 3, 4). Even after the tears in the spore coat extend to its distal surface, the spore coat can remain attached to the distal cell or its derivatives (Fig. 4). With additional enlargement of the young gametophyte the spore coat is sloughed off (Fig. 5).

The second cell division of the young gametophyte occurs in the distal cell and is parallel to the polar axis of the spore (Fig. 6). A small globular gametophyte is produced by additional cell divisions occurring in cells derived from the distal cell. The proximal cell, at least in the early stages of gametophyte development, remains undivided. The surface wall of the proximal cell is thicker than other cell walls in the young gametophyte (Fig. 6). In addition to the thicker wall, there is an accumulation of mucilage on the surface of the proximal cell (Fig. 6, arrow).

Discussion and Conclusions

The dark requirement for the germination of spores of *Helminthostachys* is the same as for spores of *Botrychium* and *Ophioglossum* in axenic culture. However, the time necessary for germination of *Helminthostachys* spores, 8 months, is longer than for other spores of the Ophioglossaceae that have been germinated in axenic culture (Whittier, 1981).

Helminthostachys spores have smaller triradiate ridges than comparable-sized spores of *Botrychium* (e.g., *B. dissectum* forma *obliquum*). The arms of the triradiate ridge are 10 μm long for *Helminthostachys* and 17 μm long for *B. dissectum*. The small triradiate ridge is probably responsible for the narrow diameter of the original protrusion of the enlarging cell during earlier germination. In *Helminthostachys* the protrusion is only about half the diameter of the spore. The protrusion in *Botrychium*, which has the larger triradiate ridge, has essentially the same diameter as the spore.

The pattern of early divisions in the young gametophytes of *Helminthostachys* is essentially the same as has been found for *Ophioglossum* and *Botrychium* (Campbell, 1907; Whittier, 1981). The first division is perpendicular to the polar axis of the spore producing proximal and distal cells. The second division occurs in the distal cell and is parallel to the polar axis of the spore. In *Botrychium* and *Ophioglossum*, the subsequent divisions in the cells derived from the distal cell produce the gametophyte (Whittier, 1981).

The proximal cell in the early stages of gametophyte development, as with *Botrychium* and *Ophioglossum* (Whittier, 1981), remains undivided. The thickened surface wall of the proximal cell and the secretion of mucilage through areas of this wall are characteristic for the Ophioglossaceae. Mucilage production

by the proximal cell has been reported for *Botrychium* (Melan, 1985) and observed in *Ophioglossum* (Whittier, unpublished).

The gametophytes of the Ophioglossaceae are slow growing (Boullard, 1963) and often live for more than one year (Jeffrey, 1897; Lang, 1902; Bruchmann, 1904; Campbell, 1911). The subterranean habitat appears to be a more protected site for these long-lived gametophytes than the soil surface. More water should be available for growth below the soil surface. Bruchmann (1906), St. John (1949), and Foster (1964) have reported finding living gametophytes in the soil during or after drought conditions. The subterranean habitat appears to provide more stable environmental conditions throughout the year which allows many of these gametophytes to be perennial.

The subterranean habitat is also important to the gametophytes of the Ophioglossaceae because they are dependent on an association with fungi in the soil for organic nutrients. In addition, the mycorrhizal fungus is also probably responsible for increasing the absorptive surface for uptake of mineral nutrients. The dependency on this mycorrhizal association occurs in early gametophyte development. The spores do not appear to contain enough reserves to support extended gametophyte growth because these young gametophytes undergo only a few cell divisions if not infected by fungi in soil (Campbell, 1907) or if no carbon energy source is available in the nutrient medium in axenic culture (Whittier, 1973). The initiation of gametophyte development in the soil would appear to increase the possibility that germinating spores and young gametophytes will be in close proximity to mycorrhizal fungi in the soil when organic nutrients are first required for development.

Evidence from this and other studies (Whittier, 1973, 1981) carried out with axenic techniques suggests that the spores of the Ophioglossaceae germinate only in the dark. Even short exposures of low light intensities are sufficient to prevent germination in *Botrychium* (Whittier, 1973). Presumably the spores sift or percolate down into the soil before germination can occur. The prevention of germination by light would be an effective mechanism to insure that germination will occur only after the spores are buried in the soil. The time delay, weeks or months, for germination in the dark probably also is important in assuring that the spores percolate to appropriate depths before germination. Since the gametophytes are adapted for the subterranean habitat, it is important for early gametophyte development to occur there.

Acknowledgments

I thank John T. Mickel (New York Botanical Garden), Donald G. Huddleston (Longwood Gardens), Edward L. Davis (University of Massachusetts), and Ronald H. Beckwith (University of Massachusetts) for supplying the spores used in this study. This study was supported in part by the Vanderbilt University Research Council.

Literature Cited

Boullard, B. 1963. Le gametophytes des Ophioglossacees. Considerations biologiques. Bull. Soc. Linn. Normandie 4:81–97.

BRUCHMANN, H. 1904. Ueber das Prothallium und die Keimpflanze von *Ophioglossum vulgatum* L. Bot. Zeitung, 2. Abt. 62:227–247.

———. 1906. Uber das Prothallium und die Sporenpflanze von *Botrychium lunaria* Sw. Flora 96:203–230.

BUYSSON, R. DU 1889. Monographie des cryptogames d'Europe. II. Filicinees. Rev. Sci. Bourbonnais Centr. France 2:153–164.

CAMPBELL, D. H. 1895. *The structure and development of mosses and ferns.* 1st ed. New York: Macmillan.

———. 1907. Studies on the Ophioglossaceae. Ann. Jard. Bot. Buitenzorg, II. 6:138–194.

———. 1911. The eusporangiatae. Carnegie Inst. Washington Pub. 140.

FOSTER, D. B. 1964. The gametophytes and embryogeny of five species of *Botrychium*. Ph.D. thesis, Cornell University, Ithaca, New York.

GIFFORD, E. M. and D. D. BRANDON. 1978. Gametophytes of *Botrychium multifidum* as grown in axenic culture. Amer. Fern J. 68:71–75.

JEFFREY, E. C. 1897. The gametophyte of *Botrychium virginianum*. Trans. Roy. Canad. Inst. 5:265–294.

LANG, W. H. 1902. On the prothalli of *Ophioglossum pendulum* and *Helminthostachys zeylanica*. Ann. Bot. (London) 16:23–56.

MELAN, M. A. 1985. Morphological and physiological changes in spores of *Botrychium dissectum* forma *obliquum* during germination. Ph.D. thesis, Vanderbilt University, Nashville, Tennessee.

NOZU, Y. 1961. The gametophyte of *Helminthostachys zeylanica* and *Ophioglossum vulgatum*. Phytomorphology 11:199–206.

PANT, D. D., D. D. NAUTIYAL, and D. R. MISRA. 1984. Gametophytes of Ophioglossaceae. Phyta Monograph 1:1–111.

ST. JOHN, E. P. 1949. The evolution of the Ophioglossaceae of the eastern United States. Quart. J. Florida Acad. Sci. 12:207–219.

WHITTIER, D. P. 1972. Gametophytes of *Botrychium dissectum* as grown in sterile culture. Bot. Gaz. (Crawfordsville) 133:336–339.

———. 1973. The effect of light and other factors on spore germination in *Botrychium dissectum*. Canad. J. Bot. 51:1791–1794.

———. 1981. Spore germination and young gametophyte development of *Botrychium* and *Ophioglossum* in axenic culture. Amer. Fern J. 71:13–19.

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Shorter Notes

A Binomial for a Common Hybrid *Lycopodium*.—The taxonomic status of *Lycopodium porophilum* Lloyd & Underwood (Lycopodiaceae) recently has been clarified by Waterway (Syst. Bot. 11:263–276, 1986). She presented convincing evidence for considering this taxon a species distinct from the similar clubmosses, *L. lucidulum* Michx. and *L. selago* L., with which it formerly had been confused. Hybrids between *L. porophilum* and *L. lucidulum* frequently are encountered. These hybrids are characterized by sterile spores and morphological characters intermediate between those of the parents. Waterway provided a helpful chart outlining the distinguishing features of these three taxa (p. 272).

The geographic range of the hybrid is wholly sympatric with the distribution of *L. porophilum* from Ohio and North Carolina west to Wisconsin, Iowa, and Arkansas. Although sterile, the hybrid reproduces readily by vegetative gemmae. On the unglaciated Appalachian Plateau in Hocking County, Ohio, the hybrid is common in habitats intermediate between those of its parents. *Lycopodium porophilum* typically is restricted to the upper portions of massive sandstone exposures; *L. lucidulum* grows on talus and soil at the foot of the cliffs and on alluvial terraces of small streams. The hybrid occurs both with *L. porophilum* and also on lower portions of the same rock faces. In the mesic coves of southeast Ohio, populations of the hybrid frequently are more extensive and vigorous than colonies of either parent. The hybrid plants usurp the space on the cliffs and ledges which is available to *L. porophilum*. This preemption of its habitat apparently is a significant factor in the present rarity of *L. porophilum* in Ohio. I have not seen the hybrid growing in soil with *L. lucidulum*.

Since this hybrid clubmoss is so common and widespread, it seems useful to provide it with a binomial to replace a cumbersome formula.

Lycopodium* ×*bartleyi Cusick, hybr. nov.—Type: Ohio, Hocking Co., mossy sandstone boulders above Keifel Rd, 0.3 mi NE, jct of Big Pine Creek Rd, Sect 7, Benton Township, 18 March 1987, *Cusick 26204* (OS; isotypes MICH, MU).

Hybrida e *Lycopodio lucidulo* et *L. porophilo* exorta, aliis characteribus inter parentes media, sporis abortivis.

The epithet honors Floyd Bartley (1884–1974) of Circleville, Ohio, who collected thousands of plant specimens—including this hybrid—from southeast Ohio from the 1930s through the 1960s. Stuckey (Ohio J. Sci. 75:209–210, 1975) summarized Bartley's contributions to our knowledge of the Ohio flora.

Thanks to Kerry Barringer, Brooklyn Botanic Garden, for checking the Latin diagnosis.—Allison W. Cusick, Division of Natural Areas and Preserves, Ohio Department of Natural Resources, Columbus, OH 43224.

Nomenclatural Notes on Some Ferns of Costa Rica, Panama, and Colombia.—III.—This is a continuation of the series begun a few years ago (Amer. Fern J. 67:58–60. 1977; 75:31. 1985) to record changes of names pertinent to ongoing floristic projects.

Arachniodes ochropteroides (Baker) Lellinger, comb. nov.—*Nephrodium ochropteroides* Baker, Ann. Bot. (London) 5:325. 1891.—TYPE: Jamaica, Fox's Gap, Apr 1886, *Hart* (K; isotype IJ).

This species, *A. leucostegioides* (C. Chr.) Ching, and *A. macrostegia* (Hook.) Proctor seem more closely related to *Arachniodes* than they do to *Polystichopsis*, where the first two had been placed by Morton (Amer. Fern J. 50:152, 155. 1960).

Polystichopsis seems to me to be separable from *Arachniodes* on the basis of the long, stiff, straight, colorless hairs that have cells much longer than wide and that are borne on the axes of the ovate-acuminate to narrowly triangular, usually 2-pinnate or sometimes 3-pinnate laminae. *Arachniodes* lacks long hairs (except for *A. ochropteroides*, which has long, slightly lax, pale tan hairs that have cells only slightly longer than wide and with usually obvious cross-walls; the hairs are reminiscent of those in the genus *Ctenitis*), and many species are quite glabrous; the laminae of most are relatively broader and are 4- or 5-pinnate. The genus *Polystichopsis* includes *P. chaerophylloides* (Poir.) Morton, *P. lurida* (Jenm. ex Underw. & Maxon) Morton, *P. muscosa* (Vahl) Proctor, and *P. pubescens* (L.) Morton.

Cyathea nigripes var. **brunnescens** (Barr.) Lellinger, comb. nov.—*Trichopteris nigripes* var. *brunnescens* Barr., Rhodora 78:4, f. 5–6. 1976.—TYPE: Colombia, Dept. El Valle, Río Yurumanguí, 5–50 m, *Cuatrecasas 16155-C* (US!; isotype GH!).

Cyathea stolzei A. R. Smith ex Lellinger, comb. nov.—*Trichopteris pinnata* Stolze, Amer. Fern J. 74:103, f. 2. 1984, non Roxb. ex Clarke, 1874.—TYPE: Panama, Pcia. Colón, Santa Rita Ridge road 21–26 km from the Transisthmian Highway, 500–550 m, *Knapp 5881* (MO; isotype F).

Cyathea ursina (Maxon) Lellinger, comb. nov.—*Alsophila ursina* Maxon, J. Wash. Acad. Sci. 34:48. 1944.—TYPE: Belize, Stann Creek Distr., Stann Creek Valley, Antelope Ridge, *Gentle 3197* (US!; isotype MICH).

Pecluma ptilodon var. **caespitosa** (Jenman) Lellinger, comb. nov.—*Polypodium pectinatum* var. *caespitosum* Jenman, Bull. Bot. Dept., n.s. 4:125. 1897.—TYPE: Jamaica, St. Andrew Parish, Old England, 4000 ft, *Jenman* (NY).

Phlebodium pseudoaureum (Cav.) Lellinger, comb. nov.—*Polypodium pseudoaureum* Cav., Descr. Pl. 247. 1802.—TYPE: Without locality, *Nee* (MA), examined by Christensen (Dansk Bot. Ark. 9(3):12. 1937).

The correct specific epithet, as pointed out long ago by Christensen, must be *pseudoaureum*. Although I have not seen the type specimen, the species is so distinct that Christensen could scarcely have misidentified it. This species usually has been called *Polypodium aureum* var. *areolatum* (Humb. & Bonpl. ex Willd.) C. Chr. or *Phlebodium aureum* var. *areolatum* (Humb. & Bonpl. ex Willd.) Farw.

However, it is surely an independent species, differing in range and ploidy from the true *Phlebodium aureum* (L.) J. E. Smith. *Phlebodium pseudoaureum* is widely distributed throughout tropical America, whereas *P. aureum* appears to be absent from Central America and from Colombia to Bolivia.

Tectariaceae Lellinger, fam. nov.—TYPE: *Tectaria* Cav.

Rhizomata stipitesque ad basin squamosi, squamosis angustis saepe fibrillosis concoloribus non lanceolatis vel ovatis bicoloribusque. Rhachides fuscae teres vel sulcatae, sulcis continuis non interruptis per sulcos costarum, plerumque saltem leviter pilosae, pilis multicellularibus plerumque catenatis, aliquando glabrae vel squamosae.

This family is established for the genus *Tectaria*, its close allies, including the genera *Ctenitis*, *Aenigmopteris*, *Ataxipteris*, *Psomiocarpa*, *Lastreopsis*, *Atalopteris*, *Pleocnemia*, *Pteridrys*, *Heterogonium*, *Camptodium*, and *Stenosemia*, and its more distant allies, *Pleuroderris*, *Dictyoxiphium*, *Hypoderris*, and *Amphiblestra*.

The name Tectariaceae replaces in part the illegitimate name Aspidiaceae, which is based on the illegitimate generic name *Aspidium*. Under Art. 18.1 of the present Code, such a family name cannot be conserved because it is based on an illegitimate generic name. The names Hypoderriaceae Ching and Dictyoxiphiaceae Ching are not validly published because they lack a Latin description, according to Pichi Sermolli (Webbia 25:273. 1970). I do not believe either has received a Latin description, and there is no provision in the Code to validate a family description on the basis of a validly described monotypic genus. There appear to be no other families based on these generic names. Ching applied his names to monotypic families. In contrast, the name Aspidiaceae has been used in an exceedingly broad sense far beyond my concept of Tectariaceae, for instance by Copeland (Gen. Fil. 100–154. 1947). It would be confusing to adopt it or Hypoderriaceae or Dictyoxiphiaceae for my concept of Tectariaceae.—DAVID B. LELLINGER, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560.

Terrestrial *Psilotum* in East-Central Alabama.—On 27 October 1986, plants of *Psilotum nudum* (L.) P. Beauv. (Psilotaceae) were discovered in Lee County, Alabama, at the southern extreme of the Piedmont Plateau in a mixed pine-deciduous woodland south of Loblockee Creek, near County Highway 11, about five miles north of Loachapoka. The population represents another extension of the known range of the species more than 240 kilometers inland from the Gulf Coast and is apparently a new state record. An effort to determine the extent of the population was made by several students and myself during the following week. More than 100 plants, usually in small patches of 5–10 aerial shoots/m^2, were located within an area comprising ca. 10 hectares, outside of which no additional plants were observed. Eight specimens representing the size range of shoots were transplanted to containers and moved to the Botany Greenhouses at Auburn University so that comparisons between greenhouse-protected plants and those in the field population could be made during the onset of winter. These

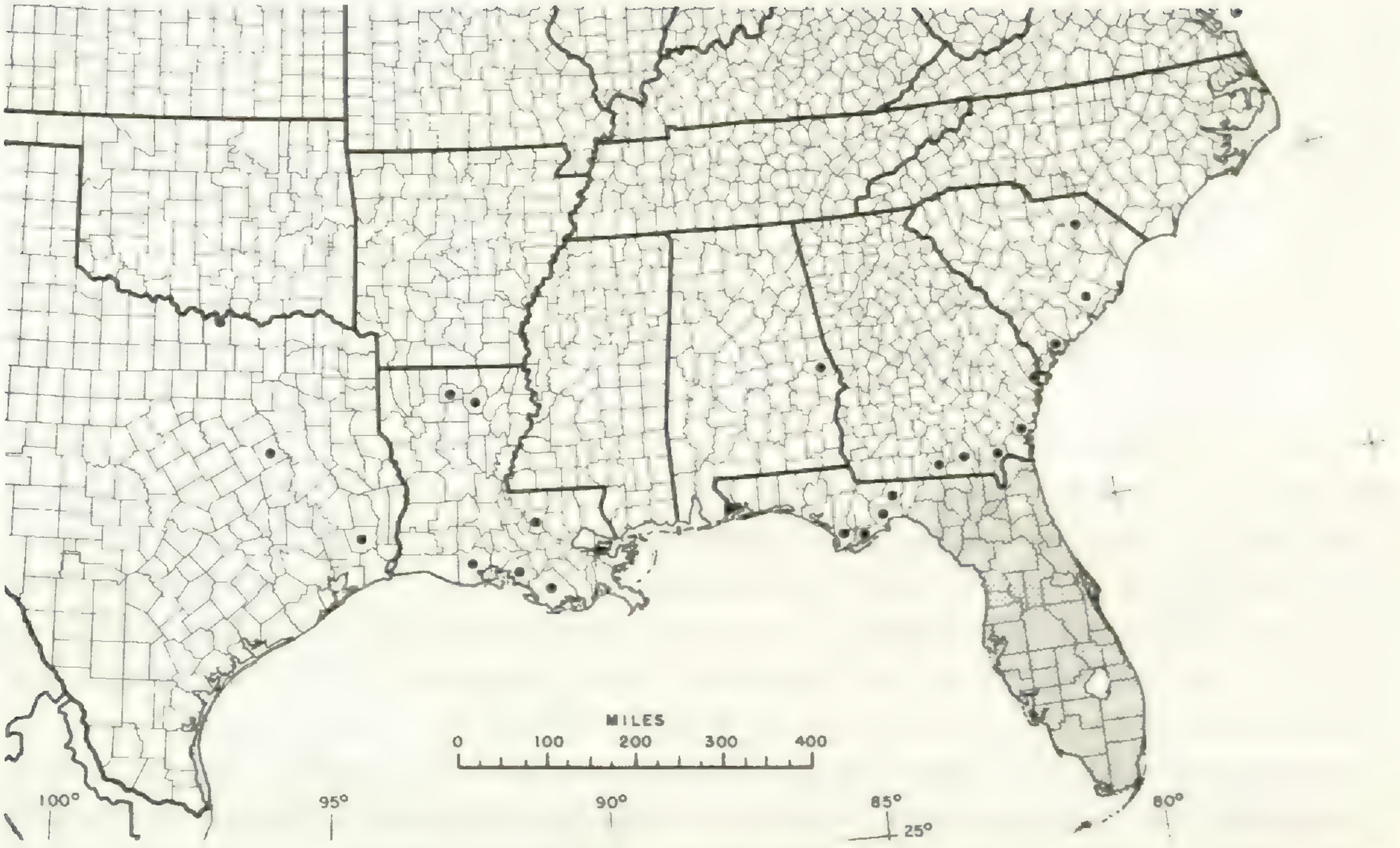

FIG. 1. County distribution of *Psilotum nudum* in the southern United States excluding peninsular Florida (shaded).

observations were continued through June 1987 when the first aerial shoots of *Psilotum* emerged in the field. Since this new locality differs markedly from most others previously reported for this species, this note will describe the habitat and discuss some aspects of this and other terrestrial populations while further studies are in progress.

Distribution of *Psilotum nudum* in the southern United States, where it reaches its northernmost limit in North America, is shown by county dots (except in peninsular Florida) in Figure 1. The other distinctly inland sites in addition to the Alabama locality reported above are: Freestone County, Texas (Lodwick, Amer. Fern J. 65:62. 1975); Lincoln Parish (Rhodes, Sida 3:525. 1970) and Ouachita Parish, Louisiana (Thieret, *Louisiana Ferns and Fern Allies*, pp. 32–33. 1980); and Darlington County, South Carolina (Radford et al., *Manual of the Vascular Flora of the Carolinas*, p. 3. 1968). The map is based upon these and various other sources (Jones et al., Sida 3:359–364. 1969; Clewell, *Guide to the Vascular Plants of the Florida Panhandle*, pp. 51–52. 1985; Snyder & Bruce, *Field Guide to the Ferns and Other Pteridophytes of Georgia*, p. 254. 1986) as well as personal observations in northern Florida. With statements such as "various habitats, epiphytic, epipetric, or terrestrial . . . ." (Radford, *loc. cit.*) or "In soil, humus, moss mats, or rotten wood in low to mesic woods" (Thieret, *loc. cit.*), certain authors generally acknowledge that *Psilotum* may grow in soil, but many imply that the species is primarily either epiphytic or grows on fallen trees, tree stumps, or palmetto bases (Lellinger, *A Field Manual of the Ferns and Fern Allies*, p. 49. 1985; Mickel, *How to Know the Ferns and Fern Allies*, p. 180. 1979). Most of the *Psilotum* sites in northern Florida, Louisiana, Texas, South Carolina, and now Alabama, too—i.e., the populations at the northern limits of the species distribution—are indeed terrestrial. Due to floristic similarities apparent between one

Louisiana locality (Rhodes, *loc. cit.*) and the one described below, one might expect additional populations to be found elsewhere, if not commonly, throughout the entire Southeast.

The Alabama site consists of formerly cultivated land that was abandoned to natural succession about 45 years ago (based upon ring counts determined for some of the largest trees and information from local residents). Shallow tillage furrows still mark the surface of the hillside that now is forested by young hardwoods and scattered pines. The larger pines were harvested for pulpwood about 18–19 years ago. The property on which most of the *Psilotum* plants were found was purchased by this writer in 1977. Although the variety of plant life at the site has been the object of my continued scrutiny for nearly a decade, no *Psilotum* specimens were observed there until 1986. Dominant overstory hardwood species are sweetgum (*Liquidambar styraciflua*), yellow-poplar (*Liriodendron tulipifera*), and northern red oak (*Quercus rubra*). Understory species include dogwood (*Cornus florida*), black walnut (*Juglans nigra*), red mulberry (*Morus rubra*), and Florida maple (*Acer saccharum* subsp. *floridanum*). The major low shrubs are Carolina buckthorn (*Rhamnus caroliniana*) and brook euonymus (*Euonymus americanus*); woody vines include Japanese honeysuckle (*Lonicera japonica*), greenbrier species (*Smilax glauca* and *S. rotundifolia*), and muscadine grape (*Vitis rotundifolia*). Perennial herbs observed during various seasons over the past ten years include *Chasmanthium sessiliflorum, Trillium underwoodii, T. cuneatum, Uvularia perfoliata, U. sessilifolia, Galium uniflorum, Botrychium virginianum, B. biternatum,* and *Asplenium platyneuron.* Plants of *C. sessiliflorum, G. uniflorum,* and the ferns dominate the herbaceous ground cover during the fall throughout the area where *Psilotum* was found.

The substrate on which the woodland described above has developed is typical of the Alabama Piedmont: red clays formed from gneissal granite. Shallow topsoil only a few centimeters thick overlays the red, rocky soil, and a heavy humus layer often 3–6 cm thick is present. Rotting pines killed by dark beetles several years ago are scattered on the forest floor, partially covered by leaf litter and humus. The underground portions of the *Psilotum* plants are located mainly within the leaf litter and uppermost organic soils.

Aerial stems of field specimens of *Psilotum* were still rather small (only 10 cm long or less) when a mild frost occurred in November 1986. Shoots of the largest specimens were branched in the typical dichotomous pattern six or more times, but several were only 2–3 cm tall and were branched once or not at all. The length of stem increments between branch points varied considerably from plant to plant, and these differences remained evident in and diagnostic for certain greenhouse specimens in growth occurring subsequent to transplantation. Most transplanted specimens remained green and apparently healthy, but three of the eight potted plants wilted and died within a week of being moved. The surviving ones showed no evident shock, continued to grow without loss of vigor, and attained heights exceeding 15 cm during the winter and spring of 1986–87. They remained sterile through the first week of October 1987. In the field, most aerial stems exposed above the leaf litter turned brown, softened, and dried out during November 1986 before any "killing" frost occurred. The pattern of deterioration

in aerial stems commonly was from the base up, the tips of some specimens remaining green well into December, when the first subfreezing temperatures of the season occurred.

Underground stems (or rhizomes) in specimens selected and dug for vouchers (deposited at AUA and MICH) were branched in the coralloid pattern typical of *Psilotum*. Withered and dried aerial stems, apparently remnants from the 1985 season, were observed to originate from both aerial and underground stems at distances ranging from 2 to 20 mm behind the location of the stem of the 1986 season. One branched rhizome with an axis 12 cm long had several other erect lateral "stubs" where stems of earlier years evidently once were borne. No living aerial stems were observed to bear sporangia in 1986, and the withered stems for the previous year also showed no sporangia. Since the fall of 1986 was unusually mild, it would seem that sporulation probably could occur only very rarely (if ever) at this location. The extensive area covered by the field population, its development in an area that formerly was cultivated, the number of plants present, and their perennial sterility (ensured by annual die-back of aerial stems) stand as a combination of factors suggesting that propagation by some asexual means may be occurring at this site.

The habitat type in which this population of *Psilotum* now exists is rather common in Alabama and other southeastern states. That this species may occupy other similar sites yet only infrequently be detected may be the actual case, but factors accounting for this possibility warrant some discussion. Due to their small size, the shoots are very inconspicuous. At the Alabama locality, they are made even more obscure because of close superficial resemblance to plants of *Smilax*, *Euonymus*, and *Galium* that are abundant, also green, short, stubby, and branched due to browsing by white-tail deer. Furthermore, it seems that the inland populations consist only of vegetative plants even as late as November. If sporulating plants should develop, they would appear only very late in the fall (or winter) when few persons familiar with *Psilotum* would likely chance upon them while conducting routine field research. Our 1986 census of the population revealed numerous vegetative shoots, but more plants were located during August and September of 1987 within the same area that had been closely checked a year earlier. In one case, in Hawaii, *Psilotum* grows as a non-green rhizomorph deep within dark lava tubes (Wagner, pers. comm.) without forming typical aerial stems or sporangia, so the species seemingly could live primarily as rhizome forms in other parts of its range, too. Only further demographic studies and observations can test this hypothetical possibility concerning the scarcity of inland collections of *Psilotum* from woodland habitats. In the meantime, features of the habitat of the only known Alabama population of *Psilotum* suggest that it may occur in (and that we should search for) other inland and upland sites.

I acknowledge with gratitude the assistance of Alvin Diamond, Susan Scott, Daureen Miller, Harland Hendricks, and Charlotte Tanner in locating plants of *Psilotum* at this locality and in determining the apparent limits of the population. I also thank Herb Wagner for his helpful comments and encouragement in preparing this report.—JOHN D. FREEMAN, Department of Botany and Microbiology, Auburn University, AL 36849.

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REVIEWS

"*Field Guide to the Ferns and Other Pteridophytes of Georgia*," by L. H. Snyder, Jr., and J. G. Bruce. 1986. 270 pp. Athens: University of Georgia Press. ISBN 0-8203-0838-2 (cloth, $25.00), ISBN 0-8203-0847-1 (paperback, $12.50).

This is an up-to-date flora of the ferns and fern allies of Georgia, patterned after its forerunner, the 1951 *Ferns of Georgia*, by McVaugh and Pyron. Much new has been added to the knowledge of Georgia ferns, and there could probably still be a few more county dots added, but this looks like 1986 state-of-the-art. Each taxon is illustrated with a full page line drawing, often with detailed insets; many are from the McVaugh and Pyron illustrations, some are new. The illustrations are representative and adequate for identification in most cases, especially with the ferns. Each taxon also has the usual description, range, and habitat, and a county dot map on the facing page for easy reference. An introductory section outlines fern morphology, physiographic regions of the state, and how to use the book. There is a combination morphology-habitat outline to genera. This substitutes for the conventional dichotomous key, which is omitted. I don't think this will be helpful, but beginners will find their way by making good use of the illustrations, and advanced fern enthusiasts probably bypass most generic keys anyway.

This is a careful treatment. Mr. Snyder, retired and not a trained biologist, thought a few years ago that it would be fun to learn a fern or two. I think he has graduated from hobbyist to semipro. Dr. Bruce knows the subject academically and thoroughly. They have made a good team. There are the usual nitpickings which one can inevitably make with a flora full of records and descriptions. I doubt that the descriptions or illustrations are adequate for *Asplenium resiliens*, *A. heteroresiliens*, and *A. heterochroum*. They are close and subtle; one may also have to resort to number of spores per sporangium—32 in *A. resiliens* and *A. heteroresiliens* and 64 in *A. heterochroum*. *Pilularia* is also known from Tennessee. In *Asplenium* and *Cystopteris* the polyploid species are referred to as "fertile hybrids" of named parents, which is an oversimplification, and confusing when "sterile hybrids" are also listed. These "fertile hybrids" would be better considered as "fertile species of hybrid origin," or as "allopolyploid species derived from named parents" as was done for *Dryopteris celsa*. Lastly, there is no discussion of the arrangement of genera. They are placed in a more or less phylogenetic sequence, except for the insertion of *Polypodium* "up front" between *Osmunda* (Osmundaceae) and *Lygodium* Schizaeaceae), and the blechnoid ferns with elongate sori with *Asplenium* and *Athyrium*; these are placed descriptively with genera having similar sori.

One of the high points of the book is the treatment of the bog clubmosses, a special research interest of Dr. Bruce and an especially confusing group on the Georgia Coastal Plain. The line drawings help but the photographic plates are all one could ask to help unravel the three species and three hybrids of the *Lycopodium alopecuroides—appressum—prostatum* complex.

Those interested in the pteridophytes of this part of the world will be glad to

see how much has changed since 1951.—A. M. EVANS, Botany Department, University of Tennessee, Knoxville, TN 37996.

"*Ferns and allied plants of Victoria, Tasmania and South Australia,*" by Betty D. Duncan and Golda Issac. 1986. 258 pp. Melbourne Univ. Press. ISBN 0-522-84262-3. Available hardcover only, exclusive U.S. distributor: International Specialized Book Services, Inc., 5602 N.E. Hassalo Street, Portland, Oregon 97213-3640. $20.00 + $2.25 postage.

This book is a field guide for naturalists, gardeners, and professional botanists. The introductory chapter makes the book understandable to the layman since it covers the fern life cycle, morphology, taxonomy, and how the dot distribution maps were prepared. In the following taxonomic chapters, the Polypodiaceae *sensu latissimo* is divided into twelve families, and genera are treated within the families. The genera are often narrowly defined, e.g., *Christella* and *Pneumatopteris* are separated from *Thelypteris*; *Polyphlebium, Macroglena,* and *Apteropteris* are separated from *Hymenophyllum* and *Trichomanes.* There are no keys to the families, but the book has two keys to the genera: 1) an illustrated, dichotomous key, and 2) a foldout tabular key that resembles a sideways dendrogram. The species treatments describe 130 pteridophytes in 53 genera. Synonyms are not listed unless widely used or controversial, as in Holttum's vs. Tryon's classification of tree ferns. The species descriptions are brief, followed by a list of the most important field characters. The discussions deal with habitats, variation, and other features of the plants, and here the authors show that they have considerable field experience as evidenced by their original observations about the ecology of ferns in the region. Each species treatment ends with notes on cultivation and a statement of world range. Following the taxonomic chapters is a nine page, illustrated chapter on growing ferns (by C. J. Goudey and R. J. Hill). The authors emphasize growing ferns from spores, special requirements of epiphytic or rupestral ferns, and problems with insects and other pests. A comprehensive bibliography, glossary of terms, and index to names conclude the book.

The book's greatest strength is its superb illustrations. Almost all the species have black and white photographs showing sori, leaf cutting, and, in many cases, habit and habitat. In addition, eight color plates, each with six pictures, are interspersed throughout the text. All the photographs are sharp, detailed, and well reproduced. I congratulate Bruce Fuhrer, the photographer, for his fine work. In addition to the photographs, line drawings are given and often show details of scales, hairs, or other features difficult to capture on film. The dust jacket is an attractive watercolor showing ten species of the region.

The book has, however, two weaknesses. First, although it covers Victoria, Tasmania, and South Australia, dot distribution maps are given only for Victoria. Second, cytological information is lacking—lamentable because such information is important in fern classification. Nevertheless, the book is well written, beautifully illustrated, and reasonably priced. I recommend it to everyone from down

under and anyone unfamiliar with the Kangaroo fern family.—ROBBIN C. MORAN, Missouri Botanical Garden, Box 299, St. Louis, MO 63166-0299.

"*Illustrations of Pteridophytes of Japan, Volume 5*" edited by S. Kurata and T. Nakaike with the cooperation of the Nippon Fernist Club. 1987. x + 818 pp. + folding map. University of Tokyo Press. Yen 14,000. ISBN 4-13-061065-1.

The fifth volume, with another hundred taxa of Japanese ferns, is as splendid as the preceding four, all of which have recevied reviews in this *Journal* [for review of preceding volume, see Amer. Fern J. 77:65. 1987]. Volume five is principally devoted to Hymenophyllaceae, Blechnaceae, Vittariaceae, *Adiantum*, *Arachniodes*, *Cyrtomium*, and *Lindsaea*.

The three beautiful color plates on two pages of frontispiece, a feature of each of the volumes, here depict species having reddish fronds, at least when young. The red pigments are presumably anthocyanins, once thought to be absent in ferns.

Names of several included species are subject to nomenclatural change, especially in Hymenophyllaceae. *Arachniodes hasseltii* has been placed in *Dryopteris* subg. *Nephrocystis* (H. Ito) Fraser-Jenkins [Bull. Brit. Mus. (Nat. Hist.), Bot. 14:197. 1986], and *Ctenitis maximowicziana* in the genus *Dryopsis* Holttum & Edwards [Kew Bull. 41:179. 1986]. All plants named *Adiantum diaphanum* Blume from Japan, S. China, and the Philippines should be called *A. setulosum* J. Smith, since the Javan species which includes Blume's type is very distinct, characterized by glabrous indusial flaps.—M. G. PRICE, Herbarium, North University Building, University of Michigan, Ann Arbor, MI 48109.

"*A key to the genera of New Zealand ferns and allied plants*," by P. J. Brownsey and T. N. H. Galloway. 1987. 31 pp. National Museum of New Zealand Miscellaneous Series no. 15. Available from the Librarian, National Museum, Private Bag, Wellington, New Zealand. NZ $5.95 (incl. postage). ISSN 0110-1447.

This publication provides an illustrated key for identifying the 66 genera of ferns and fern allies occurring in the New Zealand botanical region. Some 92 species (out of a total of 211) are illustrated by line drawings, with every genus represented by at least one illustration. Technical terms have been kept to a minimum, and all are defined in the illustrated glossary.

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American Fern Journal 77(4):109–114 (1987)

A New Fern from Western Mexico and its Bearing on the Taxonomy of the Cheilanthoid Ferns

JOHN T. MICKEL
New York Botanical Garden, Bronx, New York 10458

Throughout the history of pteridology, and in taxonomy in general, it has been stressed that the reproductive parts are conservative and taxonomically most useful. In the ferns the sori have been the focal point of taxonomic scrutiny because they seem to be dependable indicators of relationship, especially at the generic and higher levels. The vegetative parts generally vary much more and are taxonomically less dependable. Linnaeus recognized 15 genera based largely on sorus form. The general form of the sorus was examined more closely as years went on, and it was found that the same general sorus type was often reached in different ways. There was heavy reliance on the sorus until well into the present century. The sorus position was vital to Bower (1923–1928) in his construction of major phyletic lines in the ferns. The recent prevailing philosophy among pteridologists has been to use an assortment of characters, with modern studies extending to finer microscopic detail of morphological features (especially with the SEM) and chemical examination.

Thus, *Acrostichum*, originally encompassing all ferns with sporangia spread across the back of the fertile frond, now contains but three species, with other groups having acrostichoid sori, such as *Elaphoglossum*, *Bolbitis*, *Lomariopsis*, and *Polybotrya*, being recognized as having no close ties with *Acrostichum*. Similarly, species belonging at one time to *Polypodium*, with dorsal, round, exindusiate sori, included species now placed in *Grammitis*, *Thelypteris*, *Cyathea*, *Lophosoria*, *Dryopteris*, and others.

In the Adiantaceae (s.l.) there are two basic sorus types. Several genera have the sorus at the end of veins with a distinct, differentiated marginal flap, or false indusium, recurved to protect the sorus. This includes such genera as *Pteris*, *Cheilanthes*, *Pellaea*, *Doryopteris*, *Cryptogramma*, and *Llavea*.

On the other hand, "gymnogrammoid" sori, with the unprotected sporangia along the veins, are found in *Pityrogramma*, *Anogramma*, *Hemionitis*, *Bommeria*, *Antrophyum*, *Hecistopteris*, *Jamesonia*, *Eriosorus*, *Pterozonium*, *Coniogramme*, and others.

During a study of the ferns of western Mexico, the author came across a plant (Figs. A–C) that appeared to be a hybrid between two species that represent these two extremes of sorus configuration: *Hemionitis subcordata* (D. Eaton ex Davenp.) Mickel with gymnogrammoid sori (Figs. F, G) and *Cheilanthes skinneri* (Hook.) Tryon & Tryon with marginal sori (Figs. D, E).

The specimen has characters of the presumed parents (Table 1), both of wnich were present at the type locality. (*Selaginella pallescens* was the only additional pteridophyte collected there.) Most notably, the plant is intermediate in dissection

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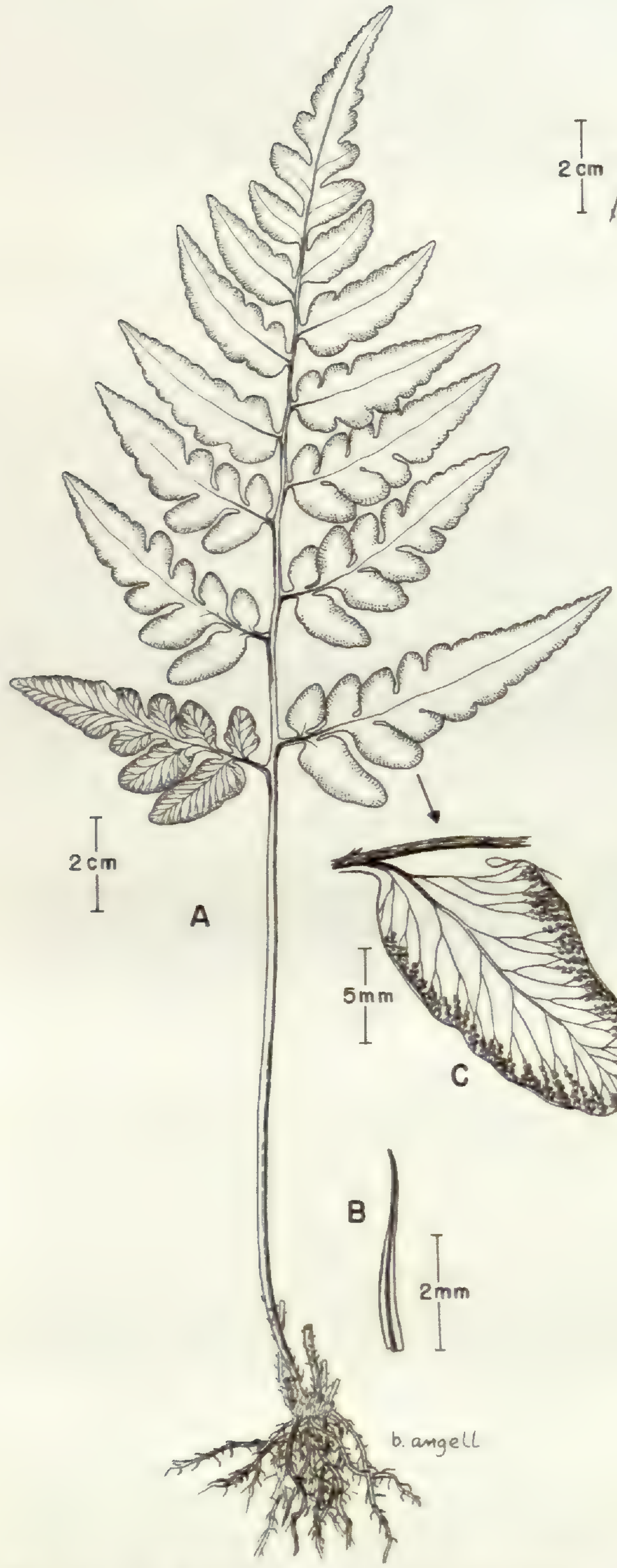

FIGS. A–C. *Cheilanthes gryphus* (*McVaugh 15908*). A, Habit. B, Rhizome scale. C, Pinnule. D, E. *Cheilanthes skinneri* (*Mickel 727*, ISC, Guerrero). D, Pinna. E, Pinnule. F, G. *Cheilanthes subcordata* (*Mickel 6241*, NY, Oaxaca). F, Pinna. G, Close-up of pinna.

TABLE 1. A Comparison of Characters in *Cheilanthes subcordata*, *C. gryphus*, and *C. skinneri*.

Character	*C. subcordata*	*C. gryphus*	*C. skinneri*
Rhizome stout, short-creeping	X	X	X
Rhizome scales bicolorous	X	X	X
Stipe tan, sulcate-winged	X	X	X
Rachis sulcate-winged	X	X	X
Blade dissection	1-pinnate	pinnate-pinnatifid to 2-pinnate	2–4-pinnate-pinnatifid
Pinnae, length of petiolule	1–3 mm	4–5(–10) mm	(6–)10–25 mm
Pinnae, number of pairs	1–4(–6)	5–7	8–12
Pinnae shape	lance-ovate, acute	lanceolate, acuminate	lance-deltate, acuminate
Pinnae basiscopically enlarged	—	X	X
Lower blade surface sparsely pubescent	X, pale	X, pale	X, green
Veins	many anastomoses	few anastomoses	free
Proximal portion of lower surface of pinna midvein	black	± black	green
Pinna margin	not modified, narrow, revolute	irregularly modified, medium width and highly modified in places	highly modified, discrete or continuous, revolute, broad
Sori	along distal ⅔ to all of vein	along distal ⅓ of vein	at vein tips
Spores	cristate	cristate	cristate
Spore size	31.5 μm	30.1 μm	31.3 μm

(nearly 2-pinnate vs. 1-pinnate and 3-pinnate in the presumed parents), the sori are limited to the distal ⅓ of the veins (vs. most of the vein length and vein ends), and the veins are casually anastomosing (vs. free and netted). On the other hand, the few spores present are well formed, so it seems to be fertile. Chromosome studies by Michael Windham have shown it to be diploid, $n = 30$ II (Ranker, in litt.). Furthermore, isozyme studies by Ranker (in litt.) show the compounds of the intermediate not to be cumulative of the presumed parents as would be expected of hybrid plants. Thus, although it is found only with its presumed parents and intermediate in several outstanding characters, it is concluded that the plant is a fertile diploid species rather than a hybrid. More work is needed, however, on reproduction in this species group.

The presumed parents of the plant in question are so distinct in their sorus configuration that it had not previously been suspected that they were closely allied. They had been placed by all taxonomists in separate genera and by some even in different families. Pichi Sermolli (1977), for example, placed *Hemionitis*

in the Hemionitidaceae and *Cheilanthes* in the Sinopteridaceae. Holttum (1947) suggested, however, that *Pityrogramma* and *Hemionitis*, although with gymnogrammoid sori, belonged with the cheilanthoid group rather than with the other gymnogrammoids, and Tryon and Tryon (1982) placed *Bommeria* and *Hemionitis* with the cheilanthoid ferns (tribe Cheilantheae), leaving *Pityrogramma* with *Jamesonia* and allies in tribe Taenitideae. On the basis of habitat, range, rhizome scales, and spore morphology, I would concur with this relationship, and the discovery of this plant suggests an even closer relationship than was previously supposed.

Neither of the presumed parents is typical of its genus. *Cheilanthes skinneri* has until recently resided in the genus *Pellaea* s.l. It was recently transferred to *Cheilanthes* (Tryon & Tryon, 1981), although it is not typical of that genus either. *Hemionitis subcordata* has been placed in *Coniogramme* and *Gymnopteris*, the latter in turn later combined with *Hemionitis* (Mickel, 1974), but it is not a typical member of that genus either, differing from most species by the subglabrous blade, crested spores and different chemistry (Mickel, 1974; Giannasi & Mickel, 1979).

Apparently, characters other than sorus position should be used to tie this small group of species together. Characters they have in common include bicolorous rhizome scales, blade indument of hairs blending to narrow scales, and perhaps most significantly segments and pinnae decurrent onto the rachis, making a single sulcus on the stipe. If indeed this is a natural and distinct group (or even genus), other species that may belong here include *Cheilanthes lozanii* (Maxon) Tryon & Tryon, which agrees in rhizome and blade indument but not decurrent segments, and *C. bolborrhiza* Mickel & Beitel, ined., which agrees in its decurrent segments but has concolorous rhizome scales and glabrous lamina.

If *Cheilanthes skinneri* and *Hemionitis subcordata* do belong to the same genus, as some common characters suggest, we do not at this time know what it would be. Because of the drastically different sori, *Cheilanthes skinneri* cannot be a *Hemionitis* and *Hemionitis subcordata* does not fit well in *Cheilanthes*. Circumscription of a distinct new genus to accommodate them both is premature until we know more about the variation of the characters in other cheilanthoid ferns, especially since there seem to be no other species that share the common characters of *C. skinneri* and *H. subcordata*.

Because of the evidence against the plant representing an intergeneric hybrid between *Cheilanthes* and *Hemionitis*, I am treating this small group within *Cheilanthes*, recognizing that it may eventually deserve generic rank. This requires a transfer of *Hemionitis subcordata* (D. Eaton ex Davenp.) Mickel:

Cheilanthes subcordata (D. Eaton ex Davenp.) Mickel, comb. nov.—*Gymnogramma subcordata* D. Eaton ex Davenp. in Rose, Contr. U.S. Natl. Herb.5: 138, t. 16. 1897.

Cheilanthes gryphus Mickel, sp. nov. (Figs. A–C).—TYPE: Mexico, Colima, low mountain summits 7 mi N of Santiago, road to Durazno, Jalisco, via the bridge over Río Cihuatlán, deciduous woodlands, 200 ft, 30 Jul 1957, *McVaugh 15908* (MICH).

Inter *Cheilanthem skinneri* et C. subcordatam notulis nonnullis intermedia.

Rhizoma horizontale compactum; paleae lineares bicolores; lamina pinnato-pinnatifida; pinnae 5–7 jugae obtuse 2–4-lobae; nervi hinc inde anastomosantes; sporangia secus venas distaliter per 2–4 mm seriatim disposita; sporae tetrahedro-globosae cristatae.

The specific epithet derives from L., *gryphus*, griffin, a hybrid between a lion and an eagle, hence an archetype of the union of incompatibles.

Rhizome horizontal, compact, 3–7 mm diam.; rhizome scales 2–3 mm long, linear, extremely slender, bicolorous, with a central, lustrous, dark castaneous to atropurpureus streak and narrow, tan margin; fronds to 46 cm tall, approximate; stipe stramineous, grayish-brown at base, with very slender, mostly bicolorous scales at base, otherwise glabrous, deeply 3-grooved, about equalling the blade in length; blade broadly lanceolate or moderately deltate, pinnate-pinnatifid to nearly bipinnate at base; pinnae 5–7 pairs, each lanceolate to deltate, acuminate, with 2–4 pairs of broad obtuse lobes, the basiscopic lobes ca. twice as long as the acroscopic ones; upper surface glabrous, lower surface with sparse straight hairs, which grade into very sparse, narrow, bicolorous scales on the rachis and pinna rachises; veins mostly free but with occasional anastomoses (2–5/pinna); sporangia running along the terminal 2–4 mm of the veins, indusium lacking, blade margin not reflexed nor modified; spores tetrahedral, crested.

Paratype: Mexico, Nayarit, S of Tepic along Hwy 200 near km post 24 between Colonias and El Refilón, mixed deciduous forest in moist, shaded gully, 8 Jul 1985, *Ranker 799* (KANU).

Several other fern genera or generic groups include taxa with highly disparate soral dispositions. *Tectaria*, with round, dorsal sori, is closely allied to *Cionidium*, which has extramarginal sori. *Polypodium*, with round, dorsal sori, is close to *Dicranoglossum* and *Neurodium* with linear, submarginal sori. *Polystichum*, with round, dorsal, indusiate sori, has a splinter *Plecosorus*, in which the indusium is lost but the sorus is protected by a differentiated margin (false indusium) as in *Cheilanthes*. *Asplenium* has elongate, dorsal sori, whereas *Diellia* and *Loxoscaphe* have sori in subterminal cups. Perhaps the most dramatic example of diverse sorus types is seen in *Tectaria* and its close relative *Dictyoxiphium*, which has linear, marginal sori, and the intergeneric cross, × *Pleuroderris michleriana*, as described in detail by Wagner et al. (1978).

Within the Adiantaceae itself there are some transitional states between marginal and gymnogrammoid sori, although they are not as dramatic as that found in *Cheilanthes gryphus* and allies. In *Adiantum* the sori, although protected by the marginal flap, are located along veins under the false indusium. In the marginal sori of *Pellaea* the sori are, in fact, somewhat elongate along the veins, sometimes a millimeter or two, and in one species, *P. bridgesii*, the sori are medial along the veins for 1–2 mm (Wagner et al., 1983). Haufler (1979) has pointed out the extreme variation of sorus length in *Bommeria*.

The case of *Cheilanthes gryphus* suggests that in this complex, at least, sorus pattern is of little taxonomic significance. We need to find new sets of characters for the generic segregation in the whole family, e.g., rhizome scales, blade indument, axis grooving, gametophyte morphology, breeding systems, and chemistry. All characters must be examined critically without heavy reliance on traditional characters.

ACKNOWLEDGMENTS

The drawings were prepared by Bobbi Angell. I am grateful to W. H. Wagner Jr., Thomas Ranker, Christopher Haufler, and Timothy Reeves for their suggestions and helpful information, to Michael Windham for the chromosome count of *Cheilanthes gryphus*, and to Rupert Barneby for his help with the Latin diagnosis.

LITERATURE CITED

BOWER, F. O. 1923–1928. *The ferns*. 3 vols. Cambridge: Cambridge Univ. Press.

GIANNASI, D. E. and J. T. MICKEL. 1979. Systematic implications of flavonoid pigments in the fern genus *Hemionitis* (Adiantaceae). Brittonia 31:405–412.

HAUFLER, C. H. 1979. A biosystematic revision of *Bommeria*. J. Arnold Arbor. 60:445–476.

HOLTTUM, R. E. 1947. A revised classification of leptosporangiate ferns. J. Linn. Soc., Bot. 53:123–158.

MICKEL, J. T. 1974. A redefinition of *Hemionitis*. Amer. Fern J. 64:3–12.

PICHI SERMOLLI, R. E. G. 1977. Tentamen pteridophytorum genera in taxonomicum ordinem redigendi. Webbia 31:313–512.

TRYON, R. M. and A. F. TRYON. 1981. Taxonomic and nomenclatural notes on ferns. Rhodora 83: 133–137.

——— and ———. 1982. *Ferns and allied plants with special reference to tropical America*. New York: Springer-Verlag.

WAGNER, W. H., JR., F. S. WAGNER, and L. D. GÓMEZ P. 1978. The singular origin of a Central American fern, *Pleuroderris michleriana*. Biotropica 10:254–264.

———, A. R. SMITH, and T. R. PRAY. 1983. A cliff brake hybrid, *Pellaea bridgesii* × *mucronata*, and its systematic significance. Madroño 30:69–83.

American Fern Journal 77(4):115–123 (1987)

The Ochreole of *Equisetum*: A Prophyllar Sheath

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The genus *Equisetum* is unique in its mode of branching. The branches are borne at the nodes, but they develop exogenously from the top of the nodal ring, alternating with the sheath segments or leaves. The branch buds develop between leaves rather than being axillary to the leaf, which is the arrangement found in seed plants, or with no relation to the leaves, as in ferns. It is obvious that the branches are associated with the node below them, rather than the node above, because if the number of leaves at a node changes, the number of branches is the same as the number of leaves below it. Although exogenous in origin, the branch bud is enclosed by the leaf sheath and must grow out through its base. Where it emerges, a fringe of sheath tissue is left around the branch base as a collar. The base of the branch is surrounded by a sheath-like structure, which differs from the regular nodal sheaths in being usually scarious, brownish in color, and unvascularized, and in lacking stomata and a subjacent internode.

This structure was described at length by Duval-Jouve (1864, as "gaîne basilaire") who followed Vaucher (1821) in considering it a protective structure for the branch bud, analogous to the bud scales of phanerogams. Milde (1867, p. 155) thoroughly discussed the "Asthülle (Ochreola)." He pointed out that it is always different in color from the branch sheaths, with short, blunt teeth. According to Milde, the ochreole does not grow from the branch but rather develops from the inner cylinder of the stem. He claimed it lacked commissures so was not of fused leaves, but of a single, toothed leaf. The outer (abaxial) angle is different from the others in being thick, with a vascular bundle, chlorophyllous cells, and scattered stomata. Thus the ochreola represents a bract with a midrib, in the axil of which the branch develops. Milde emphasized that the ochreole does not terminate an internode, as do the branch and stem sheaths. It belongs not to an internode, but rather to the whole branch. He also called attention to the similarity between this and the sheath subtending the juvenile plant as it develops from the embryo. On a later page in the same publication Milde (1867, p. 379) corrected and expanded his earlier description. The Asthülle, unlike a bract, belongs to the branch rather than the main axis, and is the first leaf whorl on the branch. He compared it to the first leaf (the prophyll) on most monocot branches.

Janczewski (1876) described the initiating bud as forming a vegetative cone and a basal portion. As the vegetative cone develops, the upper part of the basal portion is elevated to form a rim around the vegetative cone, and this rim represents the first sheath of the branch. Janczewski found Milde's interpretation of this as a bract subtending the branch very odd ("bien singulière"). DeBlock (1923) described the ochreole as membranous and becoming brown, with no trace of stomata, chlorophyll, or vascular tissue. Johnson (1937) in describing hydathodes in *Equisetum* leaves, commented on their absence on the ochreole, which is thin and usually devoid of vascular tissue. Even when vasculated, the ochreole

lacks hydathodes according to Johnson. I find no mention of the ochreole in standard morphology texts, such as Eames (1936), Smith (1938), Bierhorst (1971), Foster and Gifford (1974), or Sporne (1962).

This paper is intended to determine the accuracy of descriptions of the ochreole, to resolve discrepancies among them, and to compare the ochreole to the prophyll of seed plants.

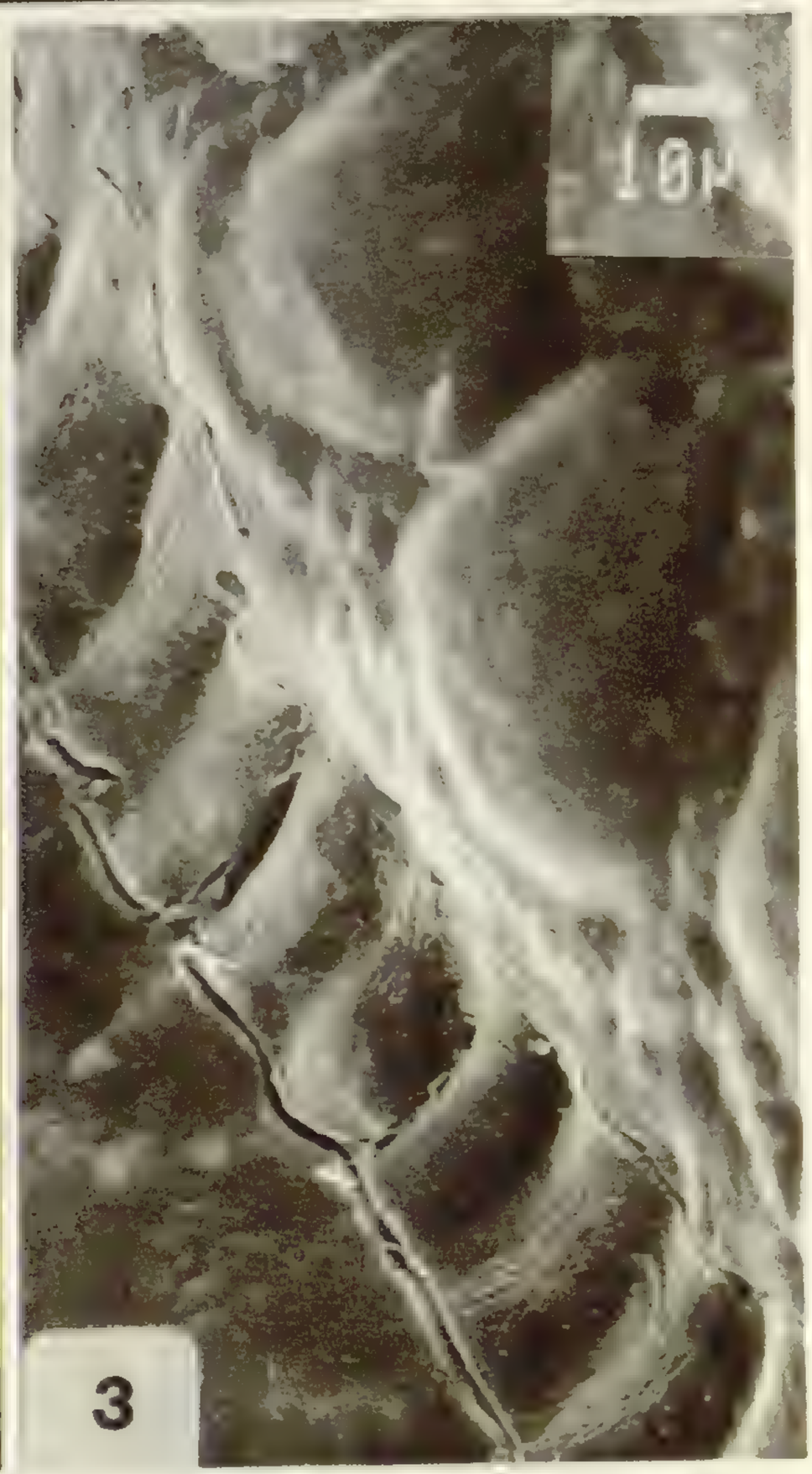
Materials and Methods

Buds of *Equisetum arvense* (*Hauke 514*, collected 1 Nov 1977) and *E. telmateia* (*Hauke C1*, collected 17 Nov 1980), and young shoots of *E. diffusum* (Univ. Rhode Island greenhouse), and *E.* ×*schaffneri* (Univ. Rhode Island greenhouse) were embedded in paraffin, serially sectioned, stained with safranin and toluidine, and studied with light microscopy. Stem nodes with branches were removed from herbarium sheets of all of the branched species of *Equisetum*, *E. ramosissimum* (*Hauke s.n.*), *E. myriochaetum* (*Hauke 238*), *E. giganteum* (*Hauke 392*), *E. sylvaticum* (*Hauke 13*), *E. pratense* (*Hauke 40*), *E. bogotense* (*Hauke 228*), *E. palustre* (*Hauke 51*), *E. fluviatile* (*Hauke 43*), *E. arvense* (*Hauke 45*), *E. telmateia* (*Hauke C1*), *E. diffusum* (*Hauke s.n.*), and *E.* ×*litorale* (*Hauke 44*), all in KIRI. These were soaked in detergent to hydrate, cleared with 10% aqueous KOH, stained with tannic acid and ferric chloride, then dehydrated in ethanol. The ochreoles were removed from the nodes, mounted on slides in diaphane under a cover slip, and examined for vasculation, commissures, stomata, and other features expected in sheaths. Photographs were made on Kodak Plus-x film using a Nikon Microflex UFX camera mounted on a Zeiss microscope.

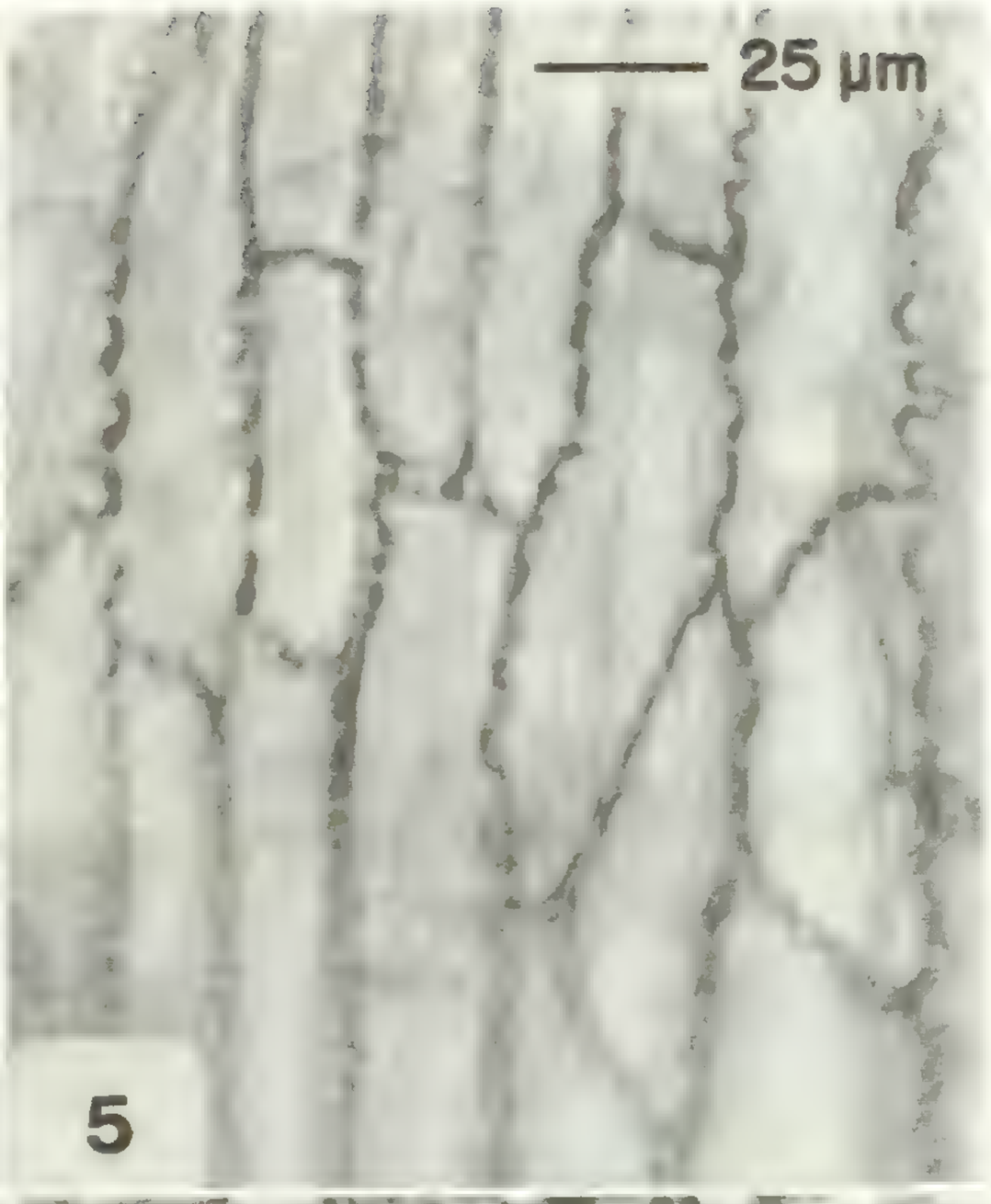
Hydrated nodes of *E. bogotense*, *E. sylvaticum*, and *E. diffusum* from the sources cited above were dehydrated with ethanol, critical point dried using liquid CO_2 in a Samdri-PVT-3B dryer, mounted on copper boats, gold-palladium coated with a Hummer II coater, and photographed on Polaroid film using a JEOL 1200 EX electron microscope in the scanning mode.

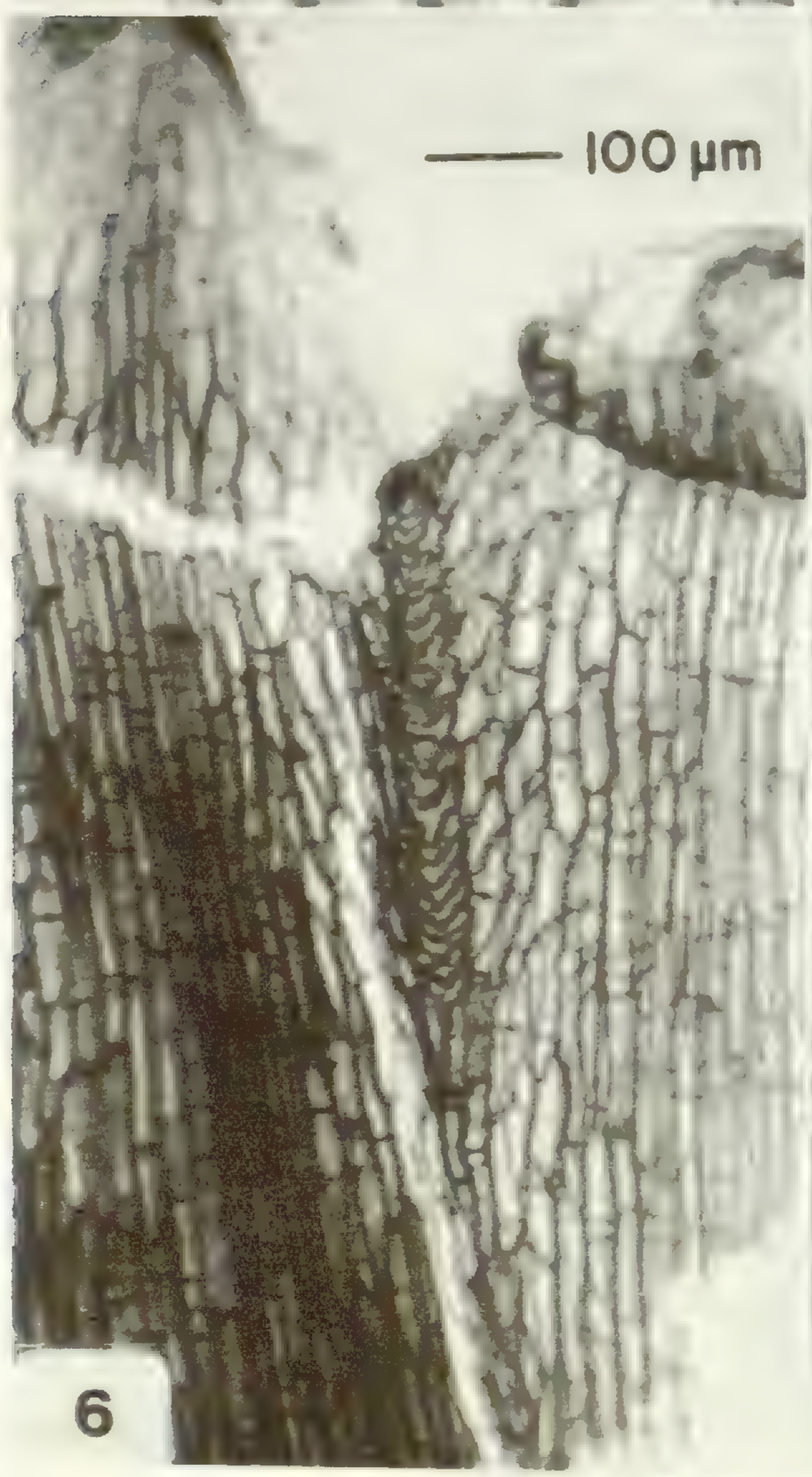
Results

Ochreoles, or basal sheaths of *Equisetum* branches, although all relatively membraneous, vary among the different species of *Equisetum*. *Equisetum diffusum* has the most complex, well-developed ochreole (Fig. 1), with prominent teeth (Fig. 2), commissures (Fig. 3), vascular strands and hydathode stomata (Figs. 4, 5) [considered to be such because they overlie the veins and are only on the adaxial surface; aerating stomata do not lie over the veins and are found only on the abaxial surface of the sheath (See Johnson, 1937)]. *Equisetum* ×*litorale* has prominent teeth, commissures, and vascular strands, but lacks stomata or hydathodes (Figs. 6, 7). *Equisetum sylvaticum* has prominent teeth with long hairs, a feature seen only in this species and stomata, but no vasculation, and obscure commissures (Figs. 8, 9). *Equisetum arvense* has prominent teeth, and *E. palustre* has prominent commissures. The other species have more rudimentary ochreoles (Fig. 10), with only *E. bogotense* showing papillae in the center of most abaxial



FIGS. 1–3. *Equisetum diffusum* ochreole. 1. Node with branches and ochreoles. 2. SEM of ochreole with basal collar (*b*), and commissure (arrow). 3. SEM of commissure.





FIGS. 4–7. Cleared ochreoles. Figures 4–5. *E. diffusum*. 4. Ochreole segment showing vascular strand and adaxial hydathode stomata. 5. As in Figure 4 but focused on abaxial epidermis. Figures 6 and 7. *Equisetum* ×*litorale*. 6. Teeth, commissure, and cells overlying vascular strand. 7. Vascular strand.

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FIGS. 8–11. Ochreole of *Equisetum*. Figures 8 and 9. SEM of *Equisetum sylvaticum*. 8. Whole ochreole with teeth bearing hairs and with basal collar (arrow). 9. Stomate (s) and a tooth hair (h). Figures 10 and 11. *Equisetum bogotense*. 10. SEM of base of branch with ochreole and basal collar (arrow). 11. **Clearing showing papillae on surface of ochreole.**

cells (Figs. 10, 11). All species studied show a basal collar formed from the outer tissues of the nodal sheath through which the branch has erupted (Figs. 2, 8, 10, 18).

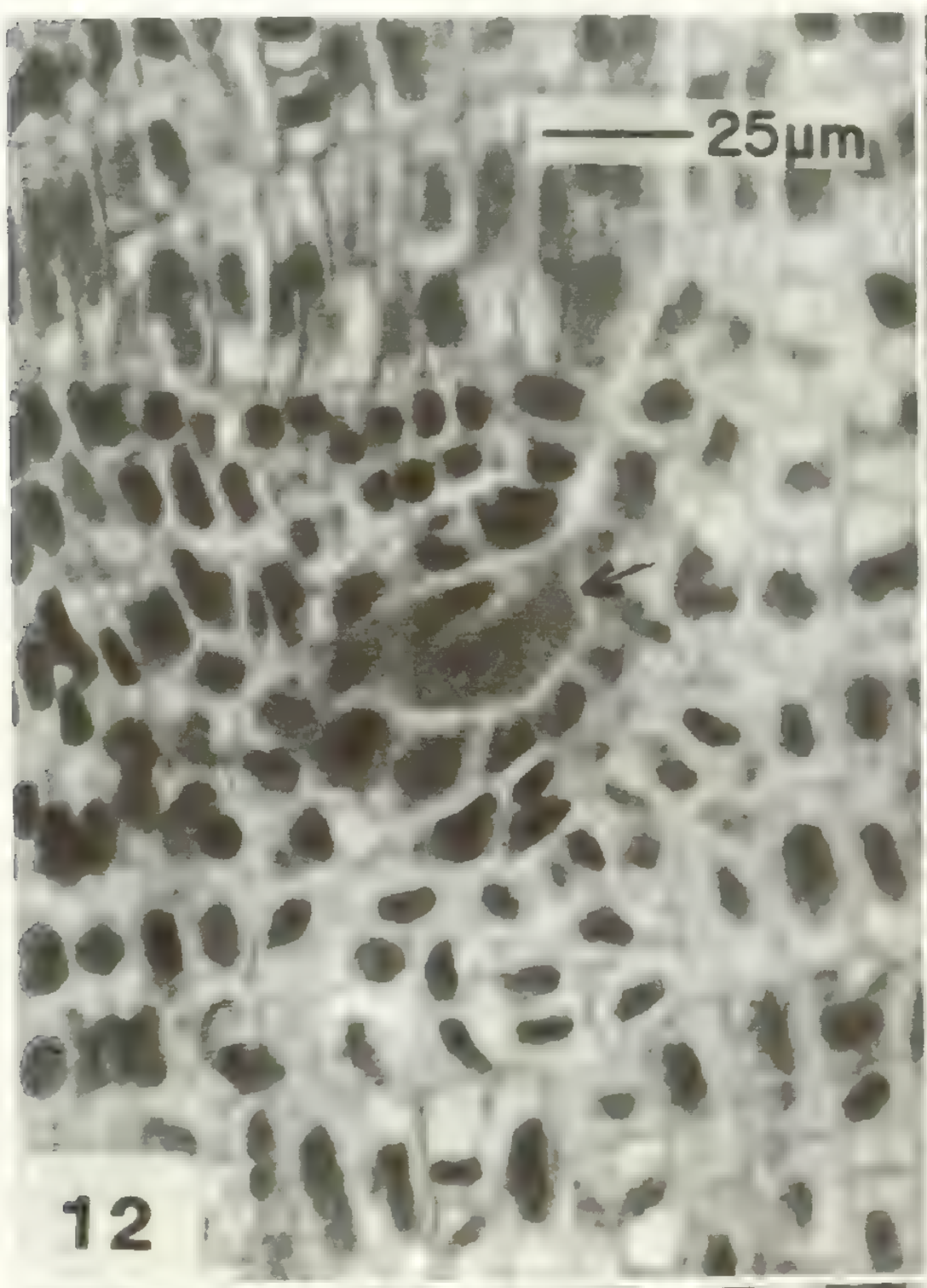
The development of the ochreole was similar in the four species studied from sectioned material, *E. diffusum*, *E. arvense*, *E. telmateia* and *E.* ×*schaffneri*. The branch is initiated by a prominent cell from the upper part of the nodal ring of the parent stem, between teeth (Fig. 12). This divides to form a pyramidal apical initial cell and several flank cells (Fig. 13). From the basal flank cells a ring forms (Fig. 14), and apical growth of this ring produces a basal sheath (Fig. 15). Also from the basal part of the branch is initiated a root apex (Fig. 15). As the branch bud develops further, the basal sheath grows longer but remains mostly 2 cell layers thick, and additional nodal rings and sheaths are initiated (Figs. 16, 17, 18). The nodal rings other than the basal one develop intercalary meristems (Figs. 17, 18). As the branch grows longer, it erupts through the sheath enclosing it (Fig. 18). The well-developed ochreole of *E. diffusum* has four segments, of which the two abaxial ones are thicker, with vascular strands, and the two adaxial ones are simpler, only 2 cell-layers thick (Figs. 19, 20).

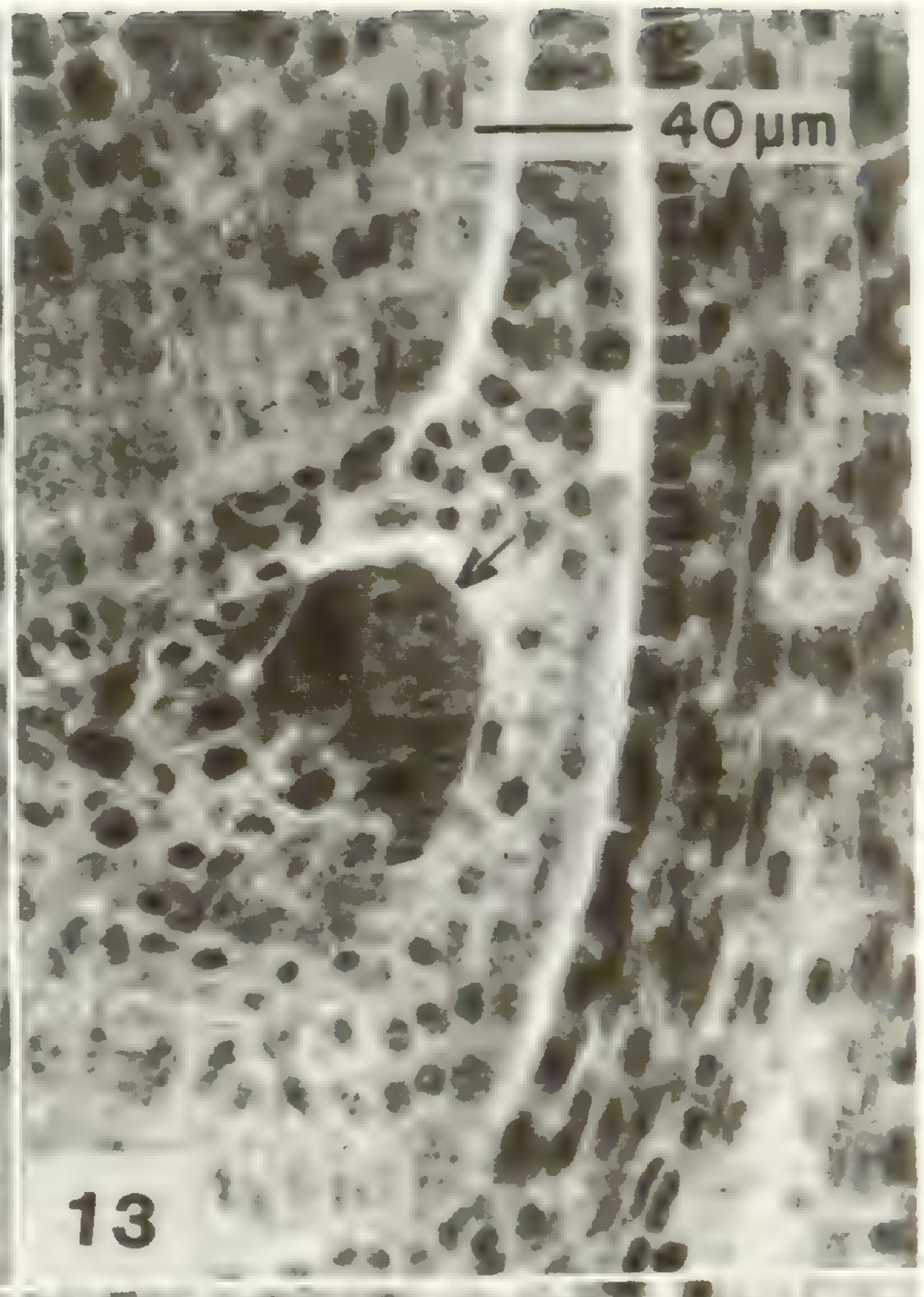
Discussion

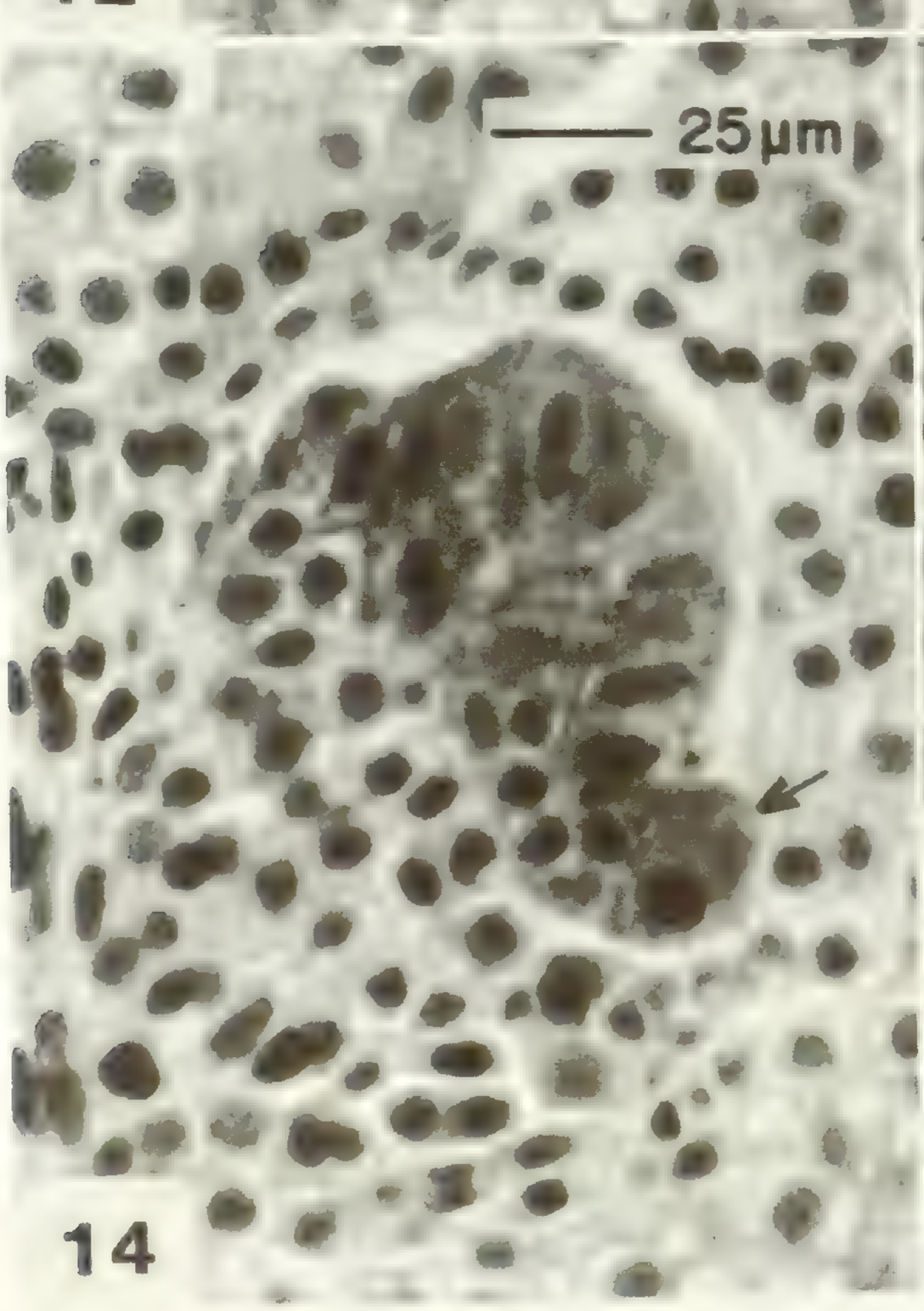
The ochreole of *Equisetum* possesses a sufficient number of sheath-like features—teeth, commissures, vascular strands, stomata, and hydathodes—to suggest its identity as the first sheath on the branch. This basal sheath is much reduced, and no one species of *Equisetum* has an ochreole that displays all of these sheath characteristics. The early ontogeny of the ochreole is also indicative of its sheath nature, with the exception of the lack of formation of an intercalary meristem and resultant subjacent internode. If DeBlock (1923) and Johnson (1937) had looked at ochreoles of additional species of *Equisetum*, they would have found vasculation, stomata, and hydathode stomata.

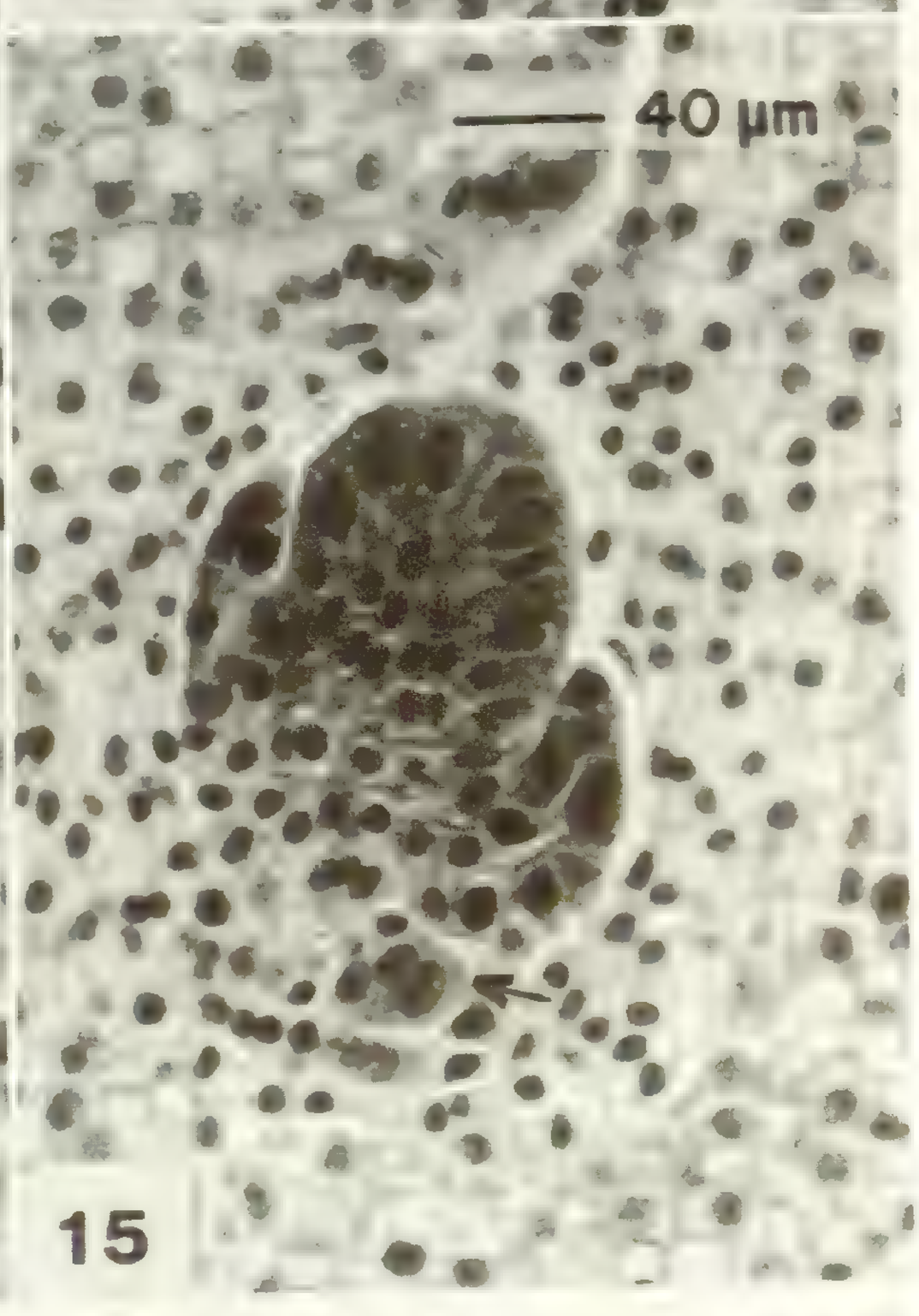
The similarity of the ochreole to the sheath subtending the juvenile plant developing from the embryo, as pointed out by Milde (1867), is dramatically clear if Figs. 15, 16 above are compared with fig. 140G in Smith (1938). Duval-Jouve (1864) analogized the basal sheath to the bud scales of seed plants. Milde (1867) compared it to the primary sheath of the embryo (the closet thing to cotyledons in this non-seed plant) and to the first leaf of a monocot branch. Both of these comparisons suggest the possibility that the ochreole should be considered a prophyll.

The ochreole does appear to fit the concept of prophyll, though that concept has never, to my knowledge, been applied to the ochreole previously. Goebel (1905) and Arber (1925) described the prophyll as the first leaf produced by a lateral branch, which usually differs from subsequent leaves on that branch. Normally, there are two prophylls in dicots and one in monocots. According to Goebel, they function to protect the bud. Guédès (1979) compared prophylls to cotyledons. "They, as it were, are the cotyledons to the branch" (p. 16) and "The main shoot first bears the cotyledons. In the same way, axillary shoots first form their prophylls. Monocotyledons have one prophyll only. Dicots have two . . ."

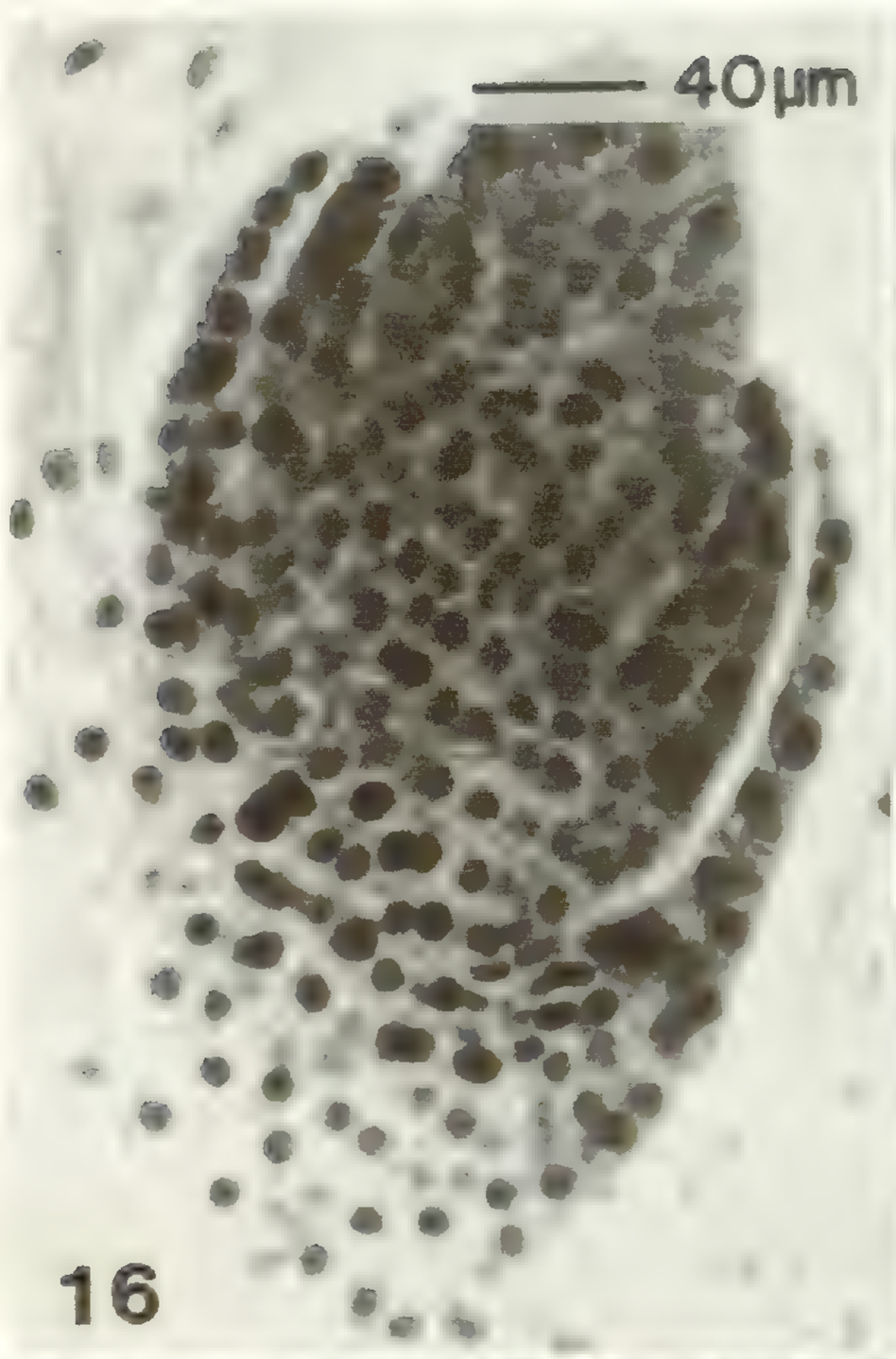








FIGS. 12–15. Longitudinal sections of young branches. Figures 12 and 13. *Equisetum arvense*. 12. Branch initial cell (arrow). 13. Branch apical dome with pyramidal apical cell (arrow). Figures 14 and 15. *Equisetum diffusum*. 14. Apex initiating ochreole (arrow). 15. Apex with ochreole and initiating root (arrow).



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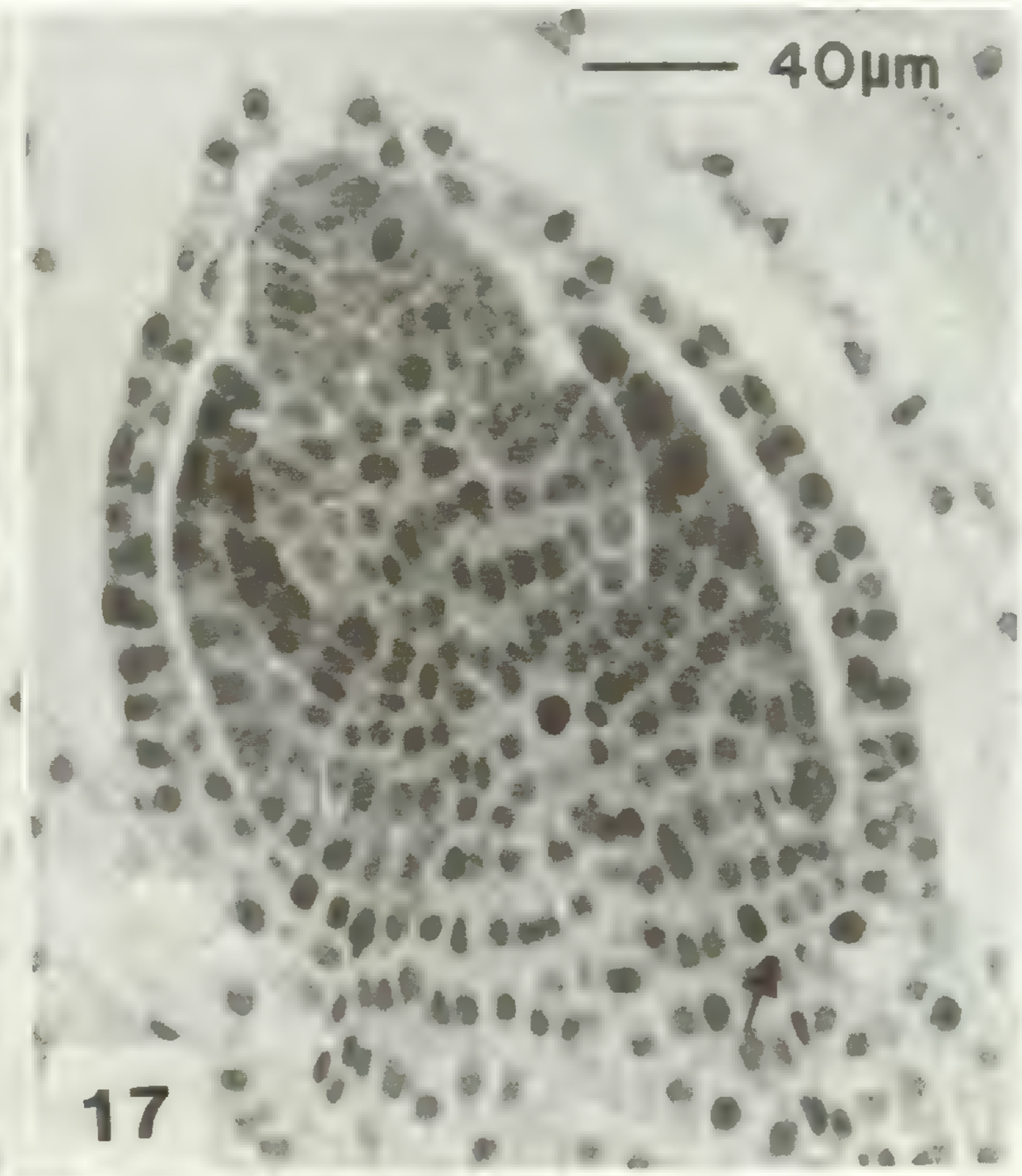

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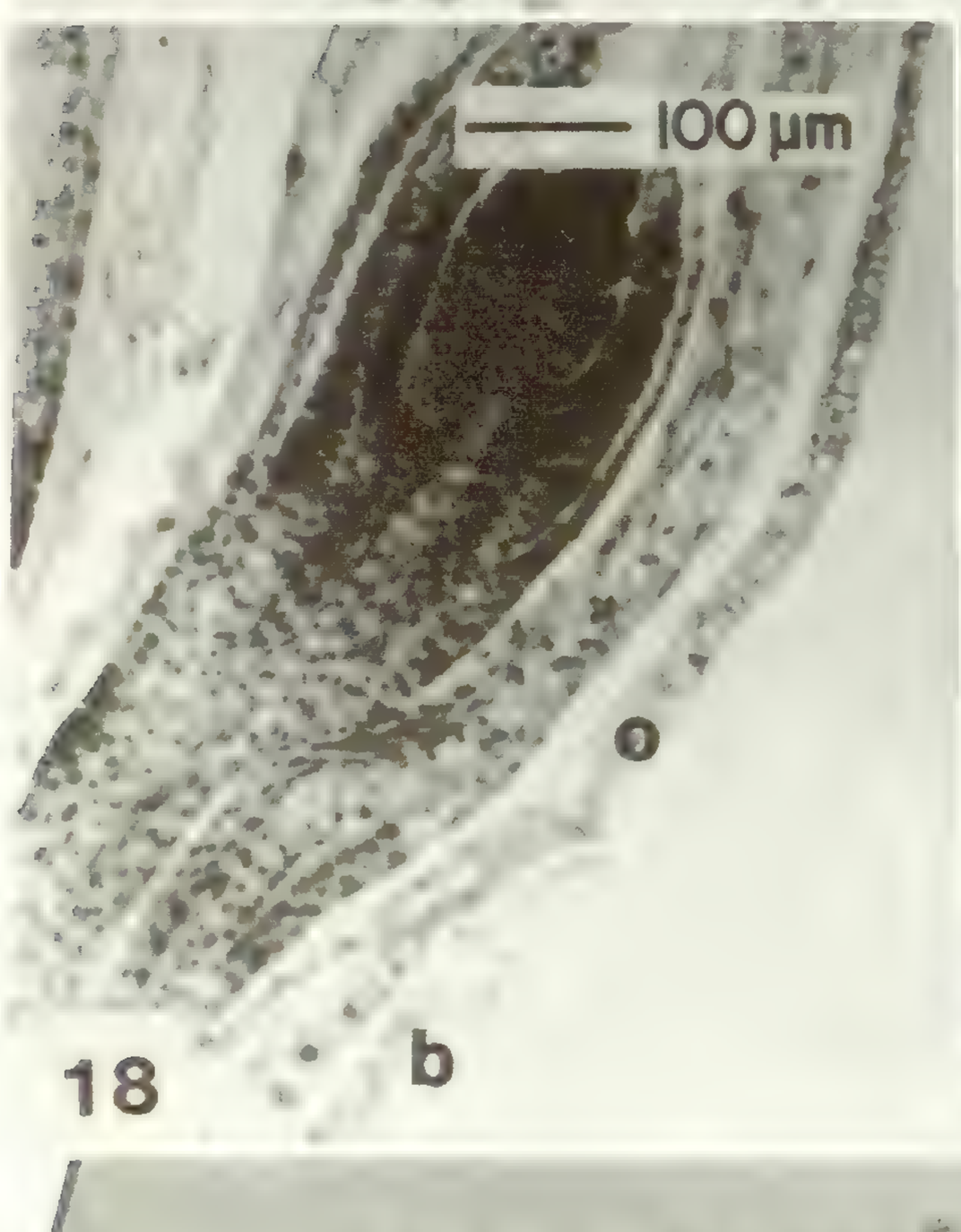

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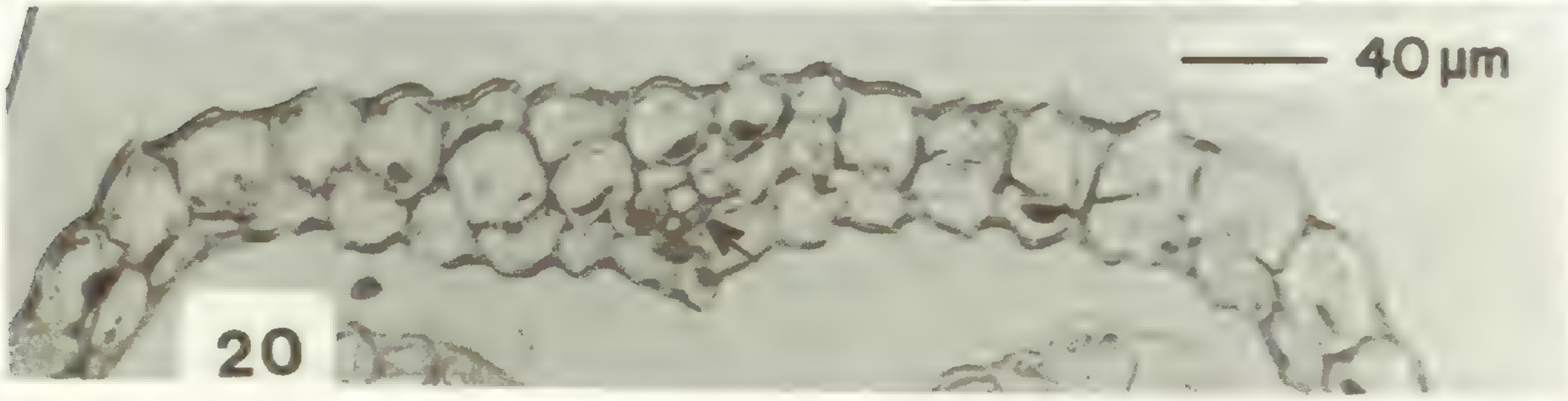

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(p. 127). Guédès described some plants as having prophylls without internodes below them, so that they are at the very base of the branch (p. 64).

The ochreole of *Equisetum* represents the first whorl of leaves on a branch, which differs from the others in being reduced and lacking a subjacent internode. It resembles the first leaves formed by the embryo, in a sense the cotyledons. All aspects of the prophyll, as seen in seed plants, are present in the ochreole of *Equisetum*, so I interpret it as a prophyllar sheath.

Literature Cited

Arber, A. 1925. *Monocotyledons*. Cambridge: University Press.

Bierhorst, D. W. 1971. *Morphology of vascular plants*. New York: The Macmillan Co.

DeBlock, L. 1923. Contribution à l'étude des Equisétacées. Thesis. Faculty of Medicine & Pharmacy, Lille.

Duval-Jouve, J. 1864. *Histoire naturelle des* Equisetum *de France*. Paris: Bailliere et Fils.

Eames, A. J. 1936. *Morphology of vascular plants. Lower groups*. New York: McGraw Hill.

Foster, A. S. and E. M. Gifford. 1974. *Comparative morphology of vascular plants*. 2nd ed. San Francisco: Freeman.

Goebel, K. 1905. *Organography of plants especially of the Archegoniatae and Spermatophyta. II. Special organography*. Translated by J. B. Balfour. Oxford: Clarendon Press.

Guédès, M. 1979. *Morphology of seed plants*. Vaduz: J. Cramer.

Janczewski, E. A. 1876. Recherches sur le développement des bourgeons dans les Prêles. Mém Soc. Sci. Nat. Cherbourg 20:69–108.

Johnson, M. A. 1937. Hydathodes in the genus *Equisetum*. Bot. Gaz. (Crawfordsville) 98:598–608.

Milde, J. 1867. Monographia Equisetorum. Nov. Actorum Acad. Caes. Leop.-Carol. German. Nat. Cur. 32(2).

Smith, G. M. 1938. *Cryptogamic botany. Vol. II. Bryophytes and pteridophytes*. New York: McGraw Hill.

Sporne, K. R. 1962. *The morphology of pteridophytes*. London: Hutchinson and Co.

Vaucher, J. P. 1821. Monographie des Prêles. Mém. Soc. Phys. Genève. 1:329–391.

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Figs. 16–20. *Equisetum diffusum* branches with ochreoles. Figures 16–18. Longitudinal sections. 16. Apex with ochreole and one nodal sheath. 17. Apex with ochreole and two nodal sheaths with intercalary meristems (arrow). 18. Branch erupting through stem sheath, with basal collar (*b*), ochreole (*o*) and five nodal sheaths with intercalary meristems. Figures 19 and 20. Cross-sections. 19. Branch with ochreole adjacent to stem with sheath. 20. Abaxial segment of ochreole with vascular strand (arrow).

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New Combinations in *Megalastrum* (Dryopteridaceae)

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One of Carl Christensen's many important contributions to fern taxonomy was demonstrating that *Dryopteris*, as defined around the turn of the century, was a vast, unrelated assemblage of ferns (Christensen, 1913, 1920). He indicated this diversity by dividing *Dryopteris* into 11 subgenera, using characters such as pinnule arrangement, hair type, and scale type that were not widely employed or appreciated by his predecessors and contemporaries. Ever since his work on *Dryopteris*, the trend has been to raise Christensen's subgenera to the generic rank or to treat them as subgenera in genera other than *Dryopteris*. In some cases, even his informal species groups have received generic status. This paper deals with one such grouping: the *D. subincisa* group of *Dryopteris* subg. *Ctenitis*.

Nowadays, all pteridologists recognize Christensen's subgenus *Ctenitis* as a distinct genus, *Ctenitis*. Within *Ctenitis* s.l., one of Christensen's informal groups, comprising the species allied to *Ctenitis protensa*, was recently established as the genus *Triplophyllum* by Holttum (1986a). He provided evidence that *Triplophyllum* is more closely allied to *Tectaria* than to *Ctenitis*. Another informal group, that of *Dryopteris subincisa*, was made a section of *Ctenitis* by Tindale (1965) and a genus by Holttum (1986b), as *Megalastrum*. We agree with Holttum that *Megalastrum* deserves generic status, as it is phenetically and cladistically distinct from *Ctenitis*. Furthermore, we are not aware of any species that is ambiguous with regard to placement in either *Megalastrum* or *Ctenitis*.

The best characteristic to distinguish *Megalastrum* from *Ctenitis* is the type of hair present on the adaxial surface of the axes. In *Megalastrum*, these hairs are coarse, whitish, multiseptate, with pointed tips, and antrorsely strigose or spreading (Fig. 1D). When dried, these hairs either remain terete or, if the cell walls collapse laterally, they all collapse in the same plane. In *Ctenitis* (and all other genera of tectarioid ferns), hairs of the above type are lacking. Rather, *Ctenitis*-hairs are present, i.e., hairs that are fine, usually blunt, reddish, erect to spreading (*never* antrorsely strigose), which when dried have cells that often collapse in planes perpendicular to the adjacent cells thereby imparting a catenate appearance to the hair, i.e., adjacent cells appear twisted relative to each other (Fig. 1C). *Megalastrum* may have *Ctenitis*-hairs on the margins and/or abaxial surface of the lamina, but never on the adaxial surface of the axes, as in all other tectarioid ferns.

Another important difference in indument is that *Ctenitis* always has unicellular, cylindrical, glandular hairs on the stalks of the sporangia (Holttum, 1986b). These glandular hairs may also occur on the margins of the indusia or on the

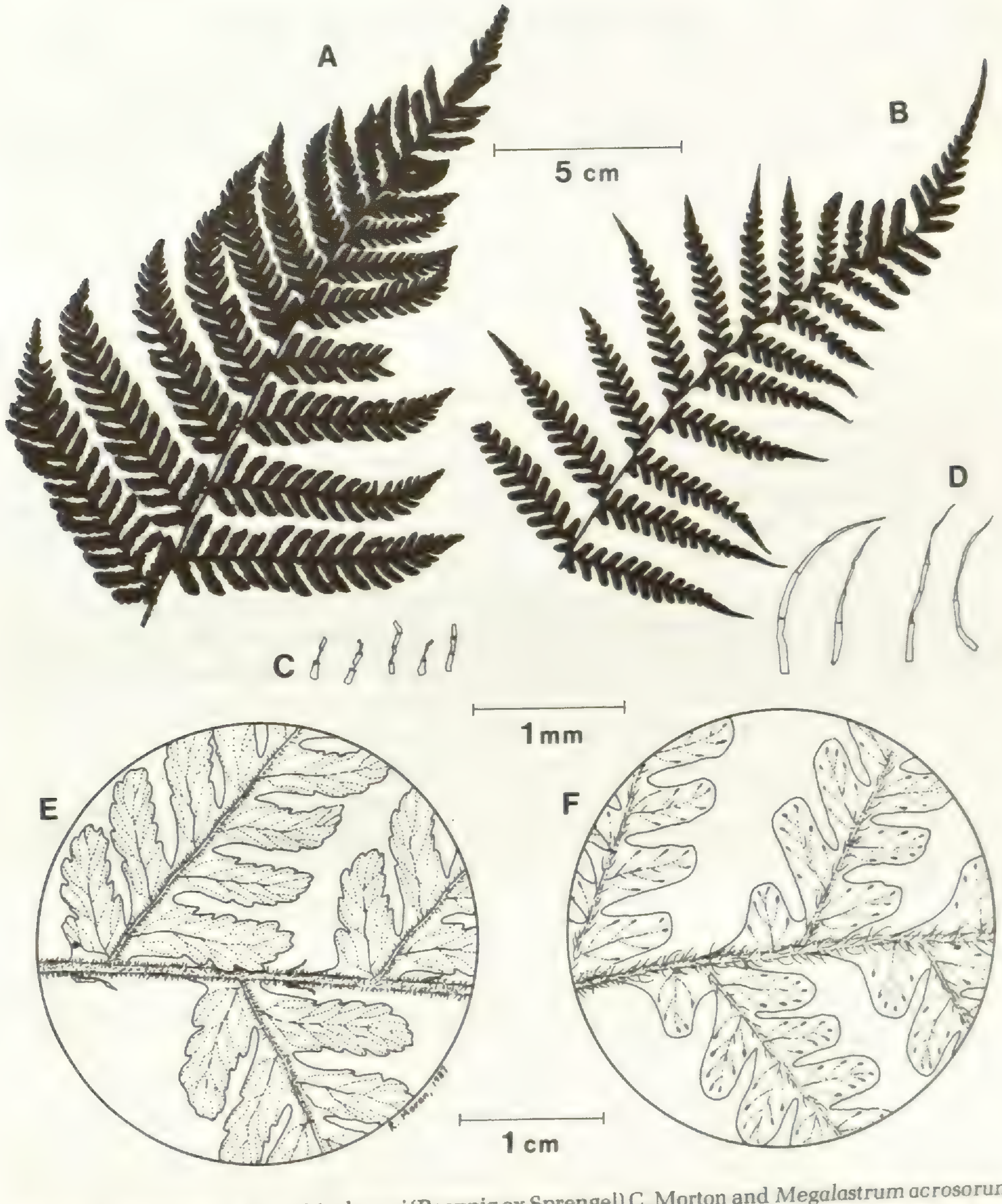

FIG. 1. **Comparison of *Ctenitis sloanei* (Poeppig ex Sprengel) C. Morton and *Megalastrum acrosorum*.** A, distal half of a proximal pinna, *C. sloanei*. B, Distal half of a proximal pinna, *M. acrosorum*; note position of the basal basiscopic lobes on the costa. C, typical *Ctenitis*-hairs from adaxial surface of the costa, *C. sloanei*. D, hairs from the adaxial surface of the costa, *M. acrosorum*. E, pinnule bases of *C. sloanei*; note the basiscopic veins arising from the costules and vein tips reaching the margin (pinna apex to the right). F, pinnule bases of *M. acrosorum*; note the basal basiscopic veins arising from the costa and clavate vein tips (pinna apex to the right). A, C, E: *Killip 2678* (MO). B, D, F: *Moran 3354* (MO).

abaxial surface of the lamina appressed to the veins. *Megalastrum* however, lacks such glandular hairs.

Megalastrum further differs from *Ctenitis* by a subtle characteristic of the venation and cutting. In *Ctenitis*, the basal basiscopic vein on the distal pinnules arises from the costule (Fig. 1E); however, in *Megalastrum* this vein arises from the costa (Fig. 1F). Concomitantly, in *Megalastrum* the basal basiscopic lobe of the distal pinnules appears broadly adnate to the costa (Figs. 1B, F). In *Ctenitis*, the basal basiscopic lobe may be decurrent on or only partially adnate to the costa, but never broadly adnate (Figs. 1A, E).

The veins in *Megalastrum* end behind the margin in conspicuous clavate tips (these are best seen on the adaxial surface). The veins in *Ctenitis* extend to the margin or may end behind the margin, but they never terminate in conspicuous clavate tips (cf. Figs. 1E, F).

Although more samples need to be examined, evidence from spore morphology supports the distinction between *Ctenitis* and *Megalastrum*. *Ctenitis* spores vary from rugose to coarsely echinate with few, stout spines (Tryon & Tryon, 1982). Two kinds of spores occur in *Megalastrum*: finely echinate (spinulose) and cristate. The echinate type, present in *M. inaequalifolium*, *M. lanuginosum* (from Africa), and *M. villosum*, is the closest to *Ctenitis* of the two types, but this type differs from *Ctenitis* by having much more numerous, narrower, and shorter spines. *Megalastrum lanuginosum* and *M. villosum* have filiform connecting strands between the bases of the spines (Holttum, 1986b, plate 3), an apparently unique feature among tectarioid ferns. The cristate spore type, present in *M. kallooi* (Jermy & Walker, 1985, fig. 11) and *M. pulverulentum* (Tryon & Tryon, 1982, fig. 67.24), has long, low, narrow, erose-margined, semiparallel wings. This spore type may be unique among tectarioid ferns, and could be formed by the coalescence of individual spines to form erose wings (Tryon & Tryon, 1982). Although distinct in their extreme forms, the echinate and cristate spore types are not fundamentally different, as evidenced by the intermediate spores of *M. connexum*, which have short, spinose wings connected at the base by filiform strands (Tryon & Tryon, 1982, fig. 67.26).

Although the foregoing character differences argue for distinguishing *Megalastrum* from *Ctenitis* solely on the basis of phenetic distance, there are also cladistic reasons for doing so. *Lastreopsis* is more closely related to *Ctenitis* than is *Megalastrum*, because *Lastreopsis* has *Ctenitis*-hairs on the adaxial surface of the axes and has unicellular, cylindrical, glandular hairs on the sporangial stalks and other parts of the plant (Tindale, 1965). Thus, since all present-day pteridologists recognize *Latreopsis*, it would be inconsistent to subsume a more distant group, *Megalastrum*, in *Ctenitis*. Given the phenetic and cladistic arguments in favor of recognizing *Megalastrum* as distinct, we make the following combinations for the neotropical taxa. No doubt there are also a number of undescribed species, especially in South America. These are best dealt within a more critical revision of *Megalastrum*. Ranges are given in general terms, mostly following Christensen (1913, 1920).

Megalastrum Holttum, Gard. Bull. Straits Settlem. 39:161. 1986.—TYPE: *Megalastrum villosum* (L.) Holttum.

Megalastrum abundans (Rosenstock) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris abundans* Rosenstock, Hedwigia 46:133. 1906.—*Ctenitis abundans* (Rosenstock) Copel. Brazil.

Megalastrum acrosorum (Hieron.) A. R. Smith & R. C. Moran, comb. nov.—*Nephrodium acrosorum* Hieron., Bot. Jahrb. Syst. 34:446. 1904.—*Ctenitis acrosora* (Hieron.) Copel. Costa Rica to Colombia.

Megalastrum adenopteris (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris adenopteris* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Afd., ser. 8. 6:85. 1920.—*Ctenitis adenopteris* (C. Chr.) Ching. Southern Brazil, N. Argentina.

Megalastrum andicola (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris andicola* (C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Afd., ser. 8. 6:88. 1920.—*Ctenitis andicola* (C. Chr.) Ching. Andes.

Megalastrum aripense (C. Chr. & Maxon) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris aripensis* C. Chr. & Maxon, J. Wash. Acad. Sci. 14:143. 1924.—*Ctenitis aripensis* (C. Chr. & Maxon) Lellinger. Trinidad.

Megalastrum atrogriseum (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris atrogrisea* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Afd., ser. 8. 6:70, fig. 15. 1920.—*Ctenitis atrogrisea* (C. Chr.) Ching. Central America.

Megalastrum bidecoratum (Lellinger) A. R. Smith & R. C. Moran, comb. nov.—*Ctenitis bidecorata* Lellinger, Proc. Biol. Soc. Wash. 98:373. 1985. Costa Rica.

Megalastrum biseriale (Baker) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium biseriale* Baker, Syn. Fil. 309. 1867.—*Ctenitis biserialis* (Baker) Lellinger. Panama, Andes.

Megalastrum canescens (Kunze ex Mett.) A. R. Smith & R. C. Moran, comb. nov.—*Phegopteris canescens* Kunze ex Mett., Abh. Senckenberg. Naturf. Ges. 2:314. 1858.—*Ctenitis canescens* (Kunze ex Mett.) C. Morton. Brazil.

Megalastrum connexum (Kaulf.) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium connexum* Kaulf., Enum. Fil. 120. 1824.—*Ctenitis connexa* (Kaulf.) Copel. Southern Brazil to Paraguay.

var. **lateadnatum** (Christ) A. R. Smith & R. C. Moran, comb. nov.—*Phegopteris lateadnata* Christ, Annuaire Conserv. Jard. Bot. Genève 3:36. 1899. Paraguay.

Megalastrum crenulans (Fée) A. R. Smith & R. C. Moran, comb. nov.—*Aspidium crenulans* Fée, Crypt. Vasc. Brés. 1:139, tab. 47, fig. 1. 1869.—*Ctenitis crenulans* (Fée) Ching. Southern Brazil, Paraguay, Venezuela.

Megalastrum eugenii (Brade) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris eugenii* Brade, Rodriguésia 13:298, tab. 2. 1940.—*Ctenitis eugenii* (Brade) Brade. Southern Brazil.

Megalstrum grande (C. Presl) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium grande* C. Presl, Del. Prag. 1:171. 1822.—*Ctenitis grandis* C. Presl) Copel. Southern Brazil.—Holttum (1986b) excluded this species from *Megalastrum* because it lacks hairs on the costae adaxially, but in all other respects it belongs here: clavate vein tips, venation and cutting, spinulose spores with a tendency for the spines to coalesce into subparallel ridges, and toothed scales. Holttum's observation that the scales of *Ctenitis grandis* are funda-

mentally different from those of *Megalastrum* in that the teeth are the outgrowths of a single cell (vs. two or more cells in *Megalastrum*) is incorrect; many of the teeth in *M. grande* are formed at the base from parts of two adjacent cells. Certainly, *M. grande* is more closely related to other species of *Megalastrum* than to any other tectarioid genus, either Old World or New World.

Megalastrum haitiense (Brause) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris subincisa* (Willd.) Urban var. *haitiensis* Brause, Ark. Bot. 17(7):67. 1922.—*Ctenitis haitiensis* (Brause) Lellinger. Haiti.

Megalastrum hirsutosetosum (Hieron.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris hirsutosetosa* Hieron., Hedwigia 46:343, tab. 6, fig. 16. 1907. Andes.

Megalastrum honestum (Kunze) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium honestum* Kunze, Linnaea 9:49. 1834.—*Ctenitis honesta* (Kunze) R. & A. Tryon. Andes.

Megalastrum inaequale (Kaulf. ex Link) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium inaequale* Kaulf. ex Link, Hort. Berol. 2:107. 1833.—*Ctenitis inaequale* (Kaulf. ex Link) Copel. Brazil.

Megalastrum inaequalifolium (Colla) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium inaequalifolium* Colla, Mem. Reale Accad. Sci. Torino 36:49. 1836.—*Ctenitis inaequalifolia* (Colla) Ching. Juan Fernández.

Megalastrum kallooi (Jermy & T. Walker) A. R. Smith & R. C. Moran, comb. nov.—*Ctenitis kallooi* Jermy & T. Walker, Bull. Brit. Mus. (Nat. Hist.), Bot. 13:267, fig. 11. 1985. Trinidad.

Megalastrum lasiernos (Sprengel) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium lasiernos* Sprengel, Syst. Veg. 4:61. 1827.—*Ctenitis lasiernos* (Sprengel) Copel. Brazil.

Megalastrum leptosorum (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris leptosora* C. Chr., Ind. Fil. 274. 1905. Andes.

Megalastrum lunense (Christ) A. R. Smith & R. C. Moran, comb. nov.—*Aspidium lunense* Christ, Bull. Herb. Boissier, sér. 2. 6:55. 1906.—*Ctenitis lunensis* (Christ) Lellinger. Costa Rica, Andes?

Megalastrum macrotheca (Fée) A. R. Smith & R. C. Moran, comb. nov.—*Phegopteris macrotheca* Fée, Mém. Fam. Foug. 11:56. 1866.—*Ctenitis macrotheca* (Fée) Ching. Lesser Antilles.

Megalastrum mollicomum (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris mollicoma* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., ser. 8. 6:75. 1920.—*Ctenitis mollicoma* (C. Chr.) Ching. Andes.

Megalastrum palmense (Rosenstock) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris subincisa* var. *palmensis* Rosenstock, Feddes Repert. Spec. Nov. Regni Veg. 22:11. 1925.—*Ctenitis palmensis* (Rosenstock) Lellinger. Costa Rica, Panama.

Megalastrum pansamalense (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris pansamalensis* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., ser. 8. 6:72. 1920.—*Ctenitis pansamalensis* (C. Chr.) Lellinger. Southern Mexico to Costa Rica.

Megalastrum platylobum (Baker) A. R. Smith & R. C. Moran, comb. nov.—

Polypodium platylobum Baker, Syn. Fil. 307. 1867.—*Ctenitis platyloba* (Baker) C. Morton. Andes, Venezuela.

Megalastrum pleiosoros (Hook. f.) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium pleiosoros* Hook. f., Trans. Linn. Soc. London, ser. 2. 20:166. 1847.—*Ctenitis pleiosoros* (Hook. f.) C. Morton. Galapagos.

Megalastrum pulverulentum (Poiret in Lam.) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium pulverulentum* Poiret in Lam., Encycl. Méth. 5:555. 1804.—*Ctenitis pulverulenta* (Poiret) Copel. Greater Antilles, S. Mexico to N. Argentina.

var. **heydei** (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris karsteniana* var. *heydei* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., ser. 8. 6:77. 1920.—*Ctenitis pulverulenta* var. *heydei* (C. Chr.) Stolze. Guatemala.

Megalastrum skutchii (Lellinger) A. R. Smith & R. C. Moran, comb. nov.—*Ctenitis skutchii* Lellinger, Proc. Biol. Soc. Wash. 98:375. 1985. Costa Rica, Panama.

Megalastrum spectabile (Kaulf.) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium spectabile* Kaulf., Enum. Fil. 121. 1824.—*Ctenitis spectabilis* (Kaulf.) Kunkel. Chile.

var. **phillippianum** (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris spectabilis* var. *phillippiana* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Afd., ser. 8. 6:70. 1920.—*Ctenitis spectabilis* var. *phillippiana* (C. Chr.) Rodriguez. Chile.

Megalastrum squamosissimum (Sodiro) A. R. Smith & R. C. Moran, comb. nov.—*Nephrodium squamosissimum* Sodiro, Anal. Univ. Quito 10(66):12. 1894. [Crypt. Vasc. Quit. 256. 1893.]—*Ctenitis squamosissima* (Sodiro) Copel. Andes.

var. **bogotense** (Hieron.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris subincisa* var. *bogotensis* Hieron., Hedwigia 46:349. 1907.

Megalastrum subincisum (Willd.) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium subincisum* Willd., L. Sp. Pl. ed. 4, 5:202. 1810.—*Ctenitis subincisa* (Willd.) Ching. Antilles, Mexico to Bolivia.

Megalastrum umbrinum (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris umbrina* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Afd., ser. 8. 6:81. 1920.—*Ctenitis umbrina* (C. Chr.) Ching. Southern Brazil, Paraguay.

Megalastrum vastum (Kunze) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium vastum* Kunze, Linnaea 9:50. 1834. Costa Rica to Bolivia.

Megalastrum villosulum (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris villosula* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Afd., ser. 8. 6:89. 1920.—*Ctenitis villosula* (C. Chr.) Ching. Bolivia.

Megalastrum villosum (L.) Holttum, Gard. Bull. Straits Settlem. 39:161. 1986. *Polypodium villosum* L., Sp. Pl. 1093. 1753.—*Ctenitis villosa* (L.) Copel. Greater Antilles.

Megalastrum wacketii (Rosenstock ex C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris wacketii* Rosenstock ex C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Afd., ser. 8. 6:84. 1920.—*Ctenitis wacketii* (Rosenstock ex C. Chr.) Ching. Southern Brazil.

Megalastrum yungense (Christ & Rosenstock) A. R. Smith & R. C. Moran, comb.

nov.—*Dryopteris yungensis* Christ & Rosenstock, Feddes Repert. Spec. Nov. Regni Veg. 5:234. 1908. Bolivia.

Literature Cited

Christensen, C. 1913. A monograph of the genus *Dryopteris*, part I. The tropical American pinnatifid-bipinnatifid species. Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Afd., ser. 7. 10:55–282.

———. 1920. A monograph of the genus *Dryopteris*, part II. The tropical American bipinnate-decompound species. Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Afd., ser. 8. 6:3–132.

Holttum, R. E. 1986a. Studies in the fern-genera allied to *Tectaria* Cav. V. *Triplophyllum*, a new genus of Africa and America. Kew Bull. 41:237–260.

———. 1986b. Studies in the fern-genera allied to *Tectaria* Cav. VI. A conspectus of genera in the Old World regarded as related to *Tectaria*, with descriptions of two genera. Gard. Bull. Straits Settlem. 39:153–167.

Jermy, A. C. and T. G. Walker. 1985. Cytotaxonomic studies of the ferns of Trinidad. 3. Descriptions of new species and hybrids and a new combination. Bull. Brit. Mus. (Nat. Hist.), Bot. 13: 251–276.

Tindale, M. D. 1965. A monograph of the genus *Lastreopsis* Ching. Contr. New South Wales Natl. Herb. 3:249–339, +23 plates.

Tryon, R. M. and A. F. Tryon. 1982. *Ferns and allied plants with special reference to tropical America*. New York: Springer-Verlag.

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Variations in Petiolar Structure of *Hypodematium crenatum*

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The importance of leaf traces in fern taxonomy has been discussed in detail by Tansley (1907, 1908), Sinnott (1911), Davie (1918), Ogura (1972), and others. Ching (1936) differentiated between *Thelypteris* and *Dryopteris* on the basis of petiolar characters. Bower (1914) used these characters along with others in establishing the relationships between *Blechnum* and allied genera. Sen (1964), Keating (1968), and Lucansky (1974a, 1974b) also used petiolar characters in working with dennstaedtioid, cyatheoid, dicksonioid, and pteroid ferns as did Bir (1962) and Kato (1972, 1975) in differentiating members of Athyriaceae. Recently, Lin and DeVol (1977, 1978) have given a key, based entirely on petiolar characters, to 170 species of Taiwan ferns and tried to establish relationships between various families of extant ferns. The above literature and many other references show that petiolar characters, particularly vascular pattern, are relatively constant within a species. In order to test constancy in Indian ferns, we have tried to study materials of the same taxon collected from diverse localities (see Khare, 1984; Khare & Shanker, 1984, 1986). In the process we noted that *Hypodematium crenatum* (Forssk.) Kuhn (Aspidiaceae of Copeland, 1947) showed considerable variation among the petioles of plants collected from different sites. A detailed study of their petioles was then begun.

MATERIALS AND METHODS

Plants of *H. crenatum* were collected from Pachmarhi (Draupadi Dweep, Handikho, and Kalakund) in Madhya Pradesh province in Central India and Almora in Uttar Pradesh province in Western Himalayas. These sites are about 1200 kilometers apart at an elevation of about 1000 meters. Plants from both places grow along road sides in shade in moist soil. Petioles were serially cut along their length and fixed in FAA. Hand or microtome sections were cut at transverse, longitudinal, and paradermal planes at 8–10 μm thickness and stained with safranin-fast green. At least ten samples from each locality were examined. Vouchers are deposited in the Herbarium of Botany Department of Allahabad University. Clearings of petioles were made by treating them in ten percent aqueous sodium hydroxide solution and chloral hydrate and subsequently staining them with safranin. To confirm the presence of lignin, cutin, tannin, starch grains, and phlobaphenes special microchemical and histochemical tests were conducted, e.g., lignin and cutin were tested by obtaining red color with phloroglucinol and sudan IV, tannin and starch grains by blue color with ferric chloride and iodine solution, respectively (see Johansen, 1940). Phlobaphene was detected by its natural yellowish brown color as suggested by Reeve (1951).

Results

Petioles of *Hypodematium crenatum* collected from both sites are yellowish green. Petiole bases are covered with large yellowish brown linear-lanceolate scales made up of uniformly thick-walled cells (Fig. 1J). Multicellular, uniseriate, elongate hairs with tapering ends occur over the entire petiole in plants of Pachmarhi (Fig. 1K). However, hair density increases gradually towards the petiole apex. Petioles of plants from Almora are glabrous. Petioles from both localities have a very shallow adaxial groove that becomes obscure distally; for most of their length petioles appear terete. In surface view the epidermal cells of a petiole appear narrow, elongate, and polygonal, with thick anticlinal walls and, occasionally, simple circular pits on their outer surface (Fig. 1I). Usually petioles are devoid of stomata, although plants collected from Almora sometimes show a few anomocytic stomata surrounded by 5–7 epidermal cells on both sides of the groove (Fig. 2J).

In transverse section petioles of plants from both sites are bounded by epidermal cells that appear small, thin-walled, and covered by a thin cuticle. The bulk of the petiole is composed of ground tissue consisting of a thick-walled lignified outer zone (3–4 layers) and several layers of thin-walled parenchymatous inner zone. Cells of the latter zone are usually filled with starch grains (Fig. 2I). Petioles of plants collected from both localities show two vascular strands at the base that are circular in plants from Pachmarhi (Figs. 1B, C, G) and slightly elongate in those from Almora (Figs. 2B, C, G). Each vascular strand is composed of a pericycle (2–3 layers) of thin-walled parenchyma cells and several layers of phloem surrounding the centrally placed xylem. The xylem is hooked in plants of Pachmarhi (Figs. 1B, C, G) but ribbon-shaped in those of Almora. The vascular strands are surrounded by a single-layered endodermis whose cells are usually filled with a dark phenolic compound phlobaphene. The two strands in the plants from Almora remain separate up to about the middle of the petiole (Fig. 2A). However, the bundles gradually become oval and the xylem become hippocampus-shaped (Figs. 2C, G). Both strands then gradually fuse with each other and form a single vascular strand for the remaining length of the petiole (Fig. 2A). During the fusion, first the endodermis (Fig. 2D) and at a slightly higher level the pericycle (Fig. 2E) and ultimately the phloem and xylem bundles of the two strands fuse, forming an almost W-shaped xylem strand with its distal arm turned inwards and surrounded completely by phloem cells. The vascular strand at this stage becomes somewhat U-shaped (Figs. 2F, H). In plants of Pachmarhi the two strands at the base fuse in the swollen basal part of the petiole (Figs. 1A, D, E), and thus there is a single strand for almost the entire petiole. This strand appears

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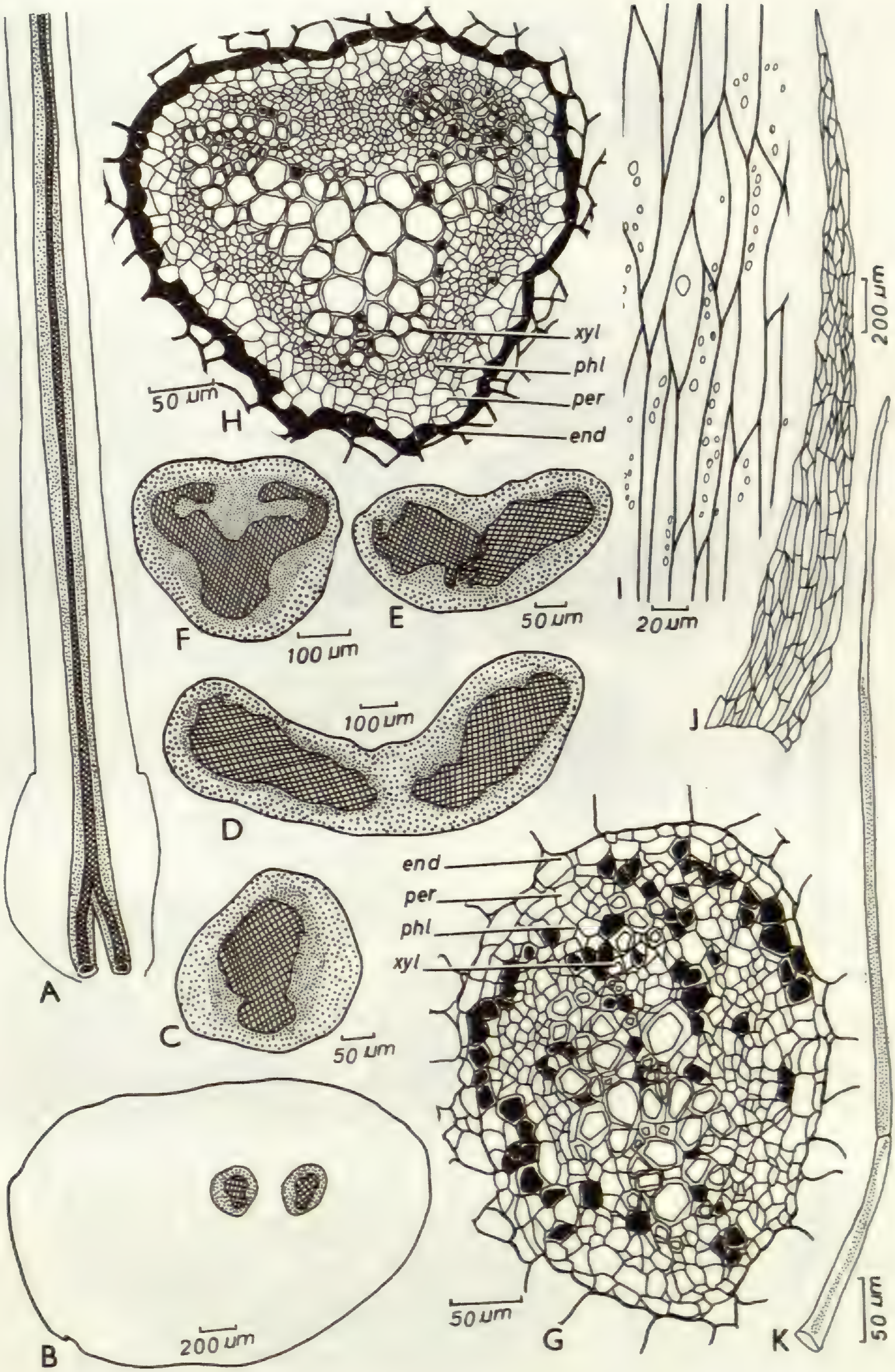
FIG. 1. *Hypodematium crenatum* from Pachmarhi. A, diagrammatic representation of course of vascular strand in the petiole. B, diagrammatic transection of petiole base showing two separate vascular strands. C–F, stages showing fusion of the two vascular strands in the swollen base of petiole. G, H, structural details of C and F respectively. I, epidermis of petiole showing pits. J, scale from petiole. K, hair from petiole. In C–F, line indicates endodermis (end), larger dots pericycle (per), finer dots phloem (phl), and hatched areas xylem (xyl).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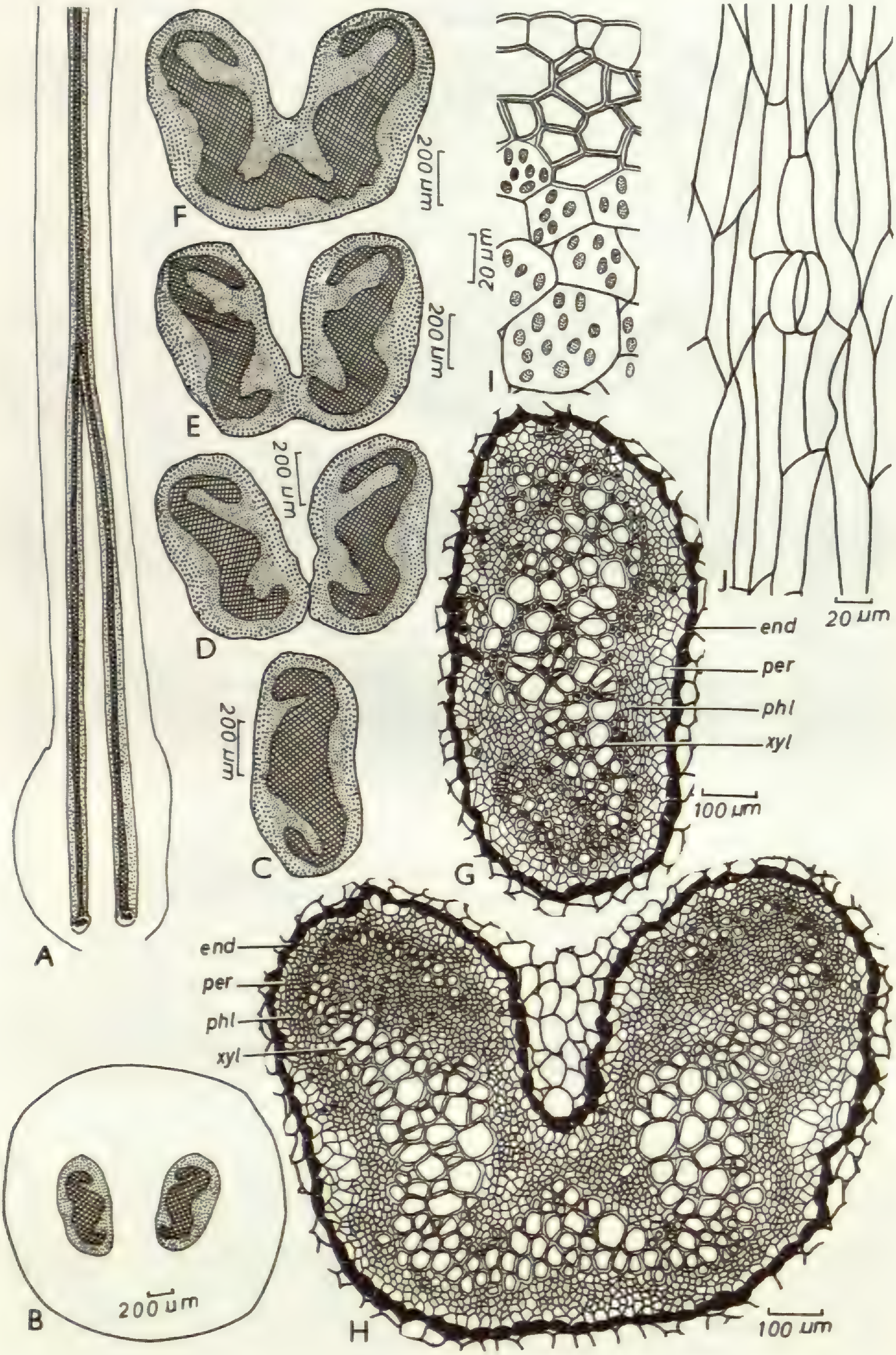
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broadly triangular with V- or Y-shaped xylem surrounded by phloem (Figs. 1F, H). The xylem in both materials is mesarch with several protoxylem points located near the free arms of xylem strands. Protoxylem elements have annular and spiral tracheids and metaxylem cells have scalariform tracheids. Phloem consists of sieve cells and parenchyma. Cells of phloem and pericycle are sometimes filled with tannin.

Discussion

In the past Mehra and Loyal (1956), Nayar and Bajpai (1970), and Loyal (1972) have vaguely described the vascular pattern in the petioles of *Hypodematium crenatum* and stated the presence of double strands. These authors have, however, neither described the details of vascular strands nor the changes they undergo at different levels. Our observations on the petioles of this taxon collected from two localities show structural as well as external differences. In other characters, e.g., rhizome, frond, epidermis, sori, and spores, plants from the two areas appear identical. Recently, Vasudeva and Bir (1982) have studied the cytology of this species from Pachmarhi and found the chromosome number ($n = 41$) identical to plants from Western Himalayas (Mehra & Loyal, 1956). Present observation on *H. crenatum* thus appears an exception to the view regarding the consistency of petiolar characters and represents, as far as we know, the first report of such variation within a species.

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Literature Cited

Bir, S. S. 1962. Taxonomy of the Indian members of family 'Aspleniaceae'. Bull. Bot. Surv. India 4:1–16.

Bower, F. O. 1914. Studies in the phylogeny of the Filicales IV. *Blechnum* and allied genera. Ann. Bot. (London) 28:363–431.

Ching, R. C. 1936. A revision of the Chinese and Sikkim-Himalayan *Dryopteris* with reference to some species from neighbouring regions. Bull. Fan Mem. Inst. Biol. 6:237–252.

Copeland, E. B. 1947. *Genera filicum*. Waltham, Massachusetts: Chronica Botanica.

Davie, R. C. 1918. A comparative list of fern pinna traces with some notes on the leaf trace in the ferns. Ann. Bot. (London) 32: 235–245.

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Fig. 2. *Hypodematium crenatum* from Almora. A, diagrammatic representation of course of vascular strands in the petiole. B, diagrammatic transection of petiole base showing two vascular strands. C–F, stages showing fusion of the two vascular strands. G, H, structural details of C and H, respectively. I, epidermis and ground tissue of petiole in transection showing starch grains. J, petiole epidermis showing a stoma. In C–F, line indicates endodermis (end), larger dots pericycle (per), finer dots phloem (phl) and hatched areas xylem (xyl).

JOHANSEN, D. A. 1940. *Plant microtechnique*. New York: McGraw-Hill.

KATO, M. 1972. The vascular structure and its taxonomic significance in the Athyriaceae. Acta Phytotax. Geobot. 25:79–91.

———. 1975. On the systematic position of *Athyrium mesosorum*. Acta Phytotax. Geobot. 27: 56–60.

KEATING, R. C. 1968. Trends of specialization in the stipe anatomy of *Dennstaedtia* and related genera. Amer. Fern J. 58:126–139.

KHARE, P. K. 1984. On the stipe of *Adiantum capillus veneris* L. and *A. venustum* Don. Pp. 21–25 in *Developmental and comparative aspects of plant structure and function*. Allahabad.

——— and R. SHANKAR. 1984. On the petiolar structure of some ferns. Pp. 257–263 in Proc. Vth Indian Geophytol. Conf., Lucknow (1983), Spl. Publ.

——— and ———. 1986. On the petiole structure of some *Adiantum* species. Geophytology 16: 54–62.

LIN, B. L. and C. E. DEVOL. 1977. The use of stipe characters in fern taxonomy I, Taiwania 22:91–99.

——— and ———. 1978. The use of stipe characters in fern taxonomy II, Taiwania 23:77–95.

LOYAL, D. S. 1972. Morphology of *Hypodematium crenatum* (Forsk.) Kuhn. Amer. Fern J. 62:88–92.

LUCANSKY, T. W. 1974a. Comparative studies of the nodal and vascular anatomy in the neotropical cyatheaceae. I. *Metaxya* and *Lophosoria*. Amer. J. Bot. 61:464–471.

———. 1974b. Comparative studies of the nodal and vascular anatomy in the neotropical Cyatheaceae. II. Squamate genera. Amer. J. Bot. 61:472–480.

MEHRA, P. N. and D. S. LOYAL. 1956. Some observations on the cytology and anatomy of *Hypodematium crenatum* (Forsk.) Kuhn. Curr. Sci. 25:363–364.

NAYAR, B. K. and N. BAJPAI. 1970. A reinvestigation of the morphology of *Hypodematium crenatum*. Amer. Fern J. 60:107–118.

OGURA, Y. 1972. *Comparative anatomy of vegetative organs of the pteridophytes*. Berlin-Stuttgart: Gebruder, Borntraeger.

REEVE, R. M. 1951. Histochemical tests for polyphenols in plants. Stain Technol. 26:91–96.

SEN, U. 1964. Importance of anatomy in phylogeny of tree-ferns and their allies. Bull. Bot. Soc. Bengal 8:26–39.

SINNOTT, E. W. 1911. The evolution of the filicinean leaf trace. Ann. Bot. (London) 25:167–191.

TANSLEY, A. G. 1907. Lectures on the evolution of the filicinean vascular system. New Phytol. 6:25–35, 53–68, 109–120, 135–147, 148–155, 187–203, 219–238, 253-269.

———. 1908. Lectures on the evolution of the filicinean vascular system. New Phytol. 7:1–16, 29–40.

VASUDEVA, S. M. and S. S. BIR. 1982. Chromosome numbers and evolutionary status of ferns and fern allies of Pachmarhi Hills (central India). Aspects of Plant Sciences 6:119–181.

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The Identity of *Hymenophyllum cristatum*

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While examining types for the "Pteridophyta of Peru" I encountered evidence of general confusion as to the identity of the Andean *Hymenophyllum cristatum* Hook. & Grev., as well as to its type specimen and early illustrations. The protologue calls attention to the principal characters that separate it from related species: "It is distinguished no less by the serrated or spinulose crested midrib and rachis, than by the large and conspicuous involucres." The accompanying illustration clearly depicts the numerous foliar toothlike processes (lamellae) that spring from the abaxial side of veins and costae, perpendicular or oblique to the plane of the lamina. Also shown is a subglobose receptacle, quite distinct from the usual elongate to turbinate receptacles seen in most related species. Morton (1968) based his section *Buesia* on ". . . having some accessory wings not in the plane of the frond" in addition to the subglobose to clavate receptacles. Within the section he included *H. cristatum* and five other species. Section *Buesia* in turn is included within the subgenus *Hymenophyllum* which is characterized by the essentially glabrous lamina and conspicuously serrate ultimate segments.

There is a type folder at the British Museum marked "*Hymenophyllum cristatum* H. & G.," with a pencilled question mark preceding the printed "Type Specimen." On the sheet (Fig. 1) are two separate specimens, neither of which are *H. cristatum*, but are instead *H. fucoides* (Sw.) Sw., a common species from the Neotropics. This species is a member of subg. *Hymenophyllum*, sect. *Ptychophyllum*, according to Morton (1968) and is quite distinct from *H. cristatum* in that it lacks any sort of lamellae on the costae or veins and the receptacles and indusia are elongate. The upper specimen is labelled *Spruce 5422.*, "*H. pedicellatum* Kze.?, in Andibus Ecuadorensibus"; the lower is annotated "Herb. John Smith, *H. fucoides* Sw." Pinned beside *Spruce 5422* is an exact copy of *t. 148*, from the Icones Filicum (Hooker & Greville, 1829). This illustrates *H. cristatum*, complete with enlargements of the subspherical indusium, globose receptacle and conspicuous lamellae. Glued beside the lower plant is a label containing exact data for the type collection of *H. cristatum* (Jameson, Mt. Cayambe, etc.). One can only assume that the drawing and Jameson label were inadvertently affixed to the wrong sheet. At any rate, neither specimen can be the type of the latter, label and attached illustration notwithstanding.

In a loan from Kew I discovered a type folder marked "*H. fucoides*" that contains a sheet (fig. 2) with two different collections, both from Hooker's herbarium. The upper left, marked "*H. fucoides*, Quito, Jameson," is not a type, but it is properly identified to species, as it has (among other characters) ovate, subentire indusia and the veins and costae lack lamellae. The right and lower plants, marked "8(2?)9, *Hymenophyllum*, Forests of the Andes," have subspherical sori, toothed indusia, many conspicuous lamellae on veins, and somewhat flexuous rachises (annotated by Morton as *H. cristatum*). Flanking a leaf of the

latter are two detailed pencil sketches, one illustrating the nearly subglobose receptacle and deeply toothed indusium, the other depicting the lamellae on the veins. Since this is apparently a Jameson specimen from Ecuador, it is very likely to be a part of the type collection of *H. cristatum*, and should be considered an isotype.

The holotype (E), part of the Greville Herbarium, simply contains two leaves of *H. cristatum*, with no mixture of other species. The label, apparently in Jameson's hand, indicates they were collected on Mt. Cayambe, east of Quito, at 15,000 ft., on trunks of trees. Above the determination, someone has lightly pencilled "=*H. fucoides*," which is a further indication of the general confusion concerning the identities of these two distinct species.

Another unfortunate product of this confusion has been the drawing (*t. 63*) used to illustrate *H. fucoides* in Hooker's *A century of ferns* (1854). Although the habit sketch and fig. 1 of this plate are somewhat representative of *H. fucoides*, fig. 2 is questionable, and fig. 3 is clearly inaccurate. Fig. 1 correctly illustrates the ovoid shape of the indusium with its denticulate margin and veins devoid of lamellae. However, the indusium shown in fig. 2 is nearly spherical, and fig. 3 shows the indusium to be laciniate and subspherical, and the veins of segments bearing a number of conspicuous lamellae. Evidently the artist produced this illustration from a mixed collection of the two species, and the solution to this riddle may be found on the sheet that contains the probable isotype of *H. cristatum* from Kew, mentioned above. The detailed sketch alongside the specimen is almost exactly reproduced (in mirror image) as Hooker's *t. 63, f. 3*. So apparently this sheet with the mixed collections of *H. cristatum* and *H. fucoides* is the very one used by the artist to produce the illustration for *t. 63* in Hooker's *A century of ferns*. Unfortunately, it was also used to illustrate *H. fucoides* in Proctor's *Ferns of Jamaica* (1985), when only the habit sketch and fig. 1 correctly apply. Thus, the identities of both species have been confused, as to type collections as well as to illustrations. It is not surprising then that some authors have placed two very different species in synonymy.

A key delineating chief differences between the two species, as well as data on types, synonyms, and the distribution of *H. cristatum* are provided below:

Lamellae lacking; sori elongate, indusia margins entire to dentate (or laciniate in var. *pedicellatum*); receptacle elongate (sometimes exserted); lamina usually compact, rarely more than 20 cm long; Neotropics . . . . . *H. fucoides* (Sw.) Sw.

Lamellae frequent and conspicuous on veins, costae and margins abaxially; sori subspherical, indusia margins laciniate; receptacle subglobose, nev-

---

←

FIGS. 1 and 2. *Hymenophyllum* types. 1, Spurious type specimen (BM) of *Hymenophyllum cristatum*, with copy of original illustration of *H. cristatum* pinned alongside upper specimen of *H. fucoides*, and piece of Jameson's original label glued next to lower specimen of *H. fucoides*. 2, Sheet (K) containing probable isotype of *Hymenophyllum cristatum* and another specimen (upper left) of *H. fucoides*.

er exserted; lamina greatly elongate, often to 30 cm long; Ecuador (also Colombia?) ..... *H. cristatum* Hook. & Grev.

Hymenophyllum cristatum Hook. & Grev., Icon. fil. 2, t. 148. 1829.—*Hymenophyllum fucoides* Sw. var. *cristatum* (Hook. & Grev.) Hieron., Hedwigia 45: 227. 1906.—*Buesia cristata* (Hook. & Grev.) Copel., Univ. Calif. Publ. Bot. 19: 296. 1941.—TYPE: Ecuador, *Jameson s.n.* (holotype E!; probable isotype K!).

Hymenophyllum sodiroi C. Chr., Index fil. 368. 1905.—*Hymenophyllum pendulum* Sod., Anal. Univ. Quito 6 (46):236. 1892 [seors.: Crypt. Vasc. Quit. 31. 1897], not Bory, 1833.—TYPE: Ecuador, "Crece en los bosques del volcán El Corazón", 3000 m, *Sodiro s.n.* (not located).

Hieronymus proposed *H. cristatum* as a variety of *H. fucoides*, citing collections of Stübel as examples: *41h, 42, 206B, 236B* (Colombia); *812, 845* (Ecuador). He claimed that these specimens agreed well with the original drawing of *H. cristatum*, calling attention to the more luxuriant leaves (up to 30 cm long), the sharply dentate indusia margins, and the thick receptacle. However no mention is made of lamellae on the veins or elsewhere. I have not seen the Stübel specimens, and it is not clear from Hieronymus' discussion whether they represent true *H. cristatum*.

Although I have not located the type of *H. sodiroi*, the original description seems to fit *H. cristatum* in every way, and I consider the two synonymous.

Distribution.—Apparently confined to Ecuador, unless the Stübel collections mentioned above add Colombia to the range.

Specimens.—ECUADOR. **Carchi:** Canton Espejo, Hda. La Rinconada, *Mexia 7458a* (UC). **Imbabura:** Lago San Marcos, Cayambe, *Cazalet & Pennington 5503* (UC). **Pichincha:** N slope of Volcán Pichincha, *Balslev et al. 1735* (UC). **Tungurahua:** SW seite des Tungurahua, 3600-3800 m, *Heinrichs 827* (F); Paramo of Minza, 3800 m, *Penland & Summers 396* (F, US); E slope of Volcán Tungurahua, 3500 m, *Rimbach 14* (F, UC, US); Cordillera Orientalis, Cubillin, 3500 m, *Rimbach 16* (UC, US).

Drs. David Lellinger (US) and Alan Smith (UC) have been most cooperative in examining specimens at their respective herbaria, to confirm the identification of duplicates of those specimens seen at F and to report additional collections not seen by me but cited above.

LITERATURE CITED

HOOKER, W. J. 1854. *A century of ferns.* London: William Pamplin.

——— and R. K. GREVILLE. 1829–1832. *Icones filicum*, vol. 2. London.

MORTON, C. V. 1968. The genera, subgenera, and sections of the Hymenophyllaceae. Contr. U.S. Natl. Herb. 38:153–214.

PROCTOR, G. R. 1985. *Ferns of Jamaica.* London: British Museum (Nat. Hist.).

Shorter Note

Two Species of *Adiantum* New to Florida.—*Adiantum tetraphyllum* Humb. & Bonpl. ex Willd. was discovered in Dade County, Florida, by A. Kesler in early 1987 from a single plant in Costello Hammock (*Nauman et al. 1881*, FTG). This represents the first occurrence of the species for Florida. The plant is growing in dense tropical hammock on exposed oolitic limestone. There is no evidence nearby (e.g., dumping) to suggest it has escaped, nor is the species cultivated in commercial or private nurseries in the immediate area. As a result, this plant appears to represent a natural range extension for the species. Outside of Florida, the species occurs in the West Indies and tropical America from Mexico southward to Brazil and Bolivia (Proctor, *Ferns of Jamaica*, 1985). It can be distinguished from the other Florida species by dull, scaly stipes and rachises and sessile or subsessile basal pinnules.

The Asian *A. caudatum* L. was found by C. Delchamps in Everglades National Park (A. Herndon, pers. comm.) as an escape on exposed limestone; these populations are now extirpated. The species has been rediscovered in the "Whispering Pines" area of Cutler in Dade County on exposed limestone in an open somewhat disturbed pineland (*Nauman 1880*, FTG). The plants have apparently escaped from cultivation nearby and at the time of this writing have disappeared from the original collection site. Since this species is common in cultivation, it is likely to escape again and be encountered by collectors. It can be distinguished from other Florida species by its 1-pinnate leaves and elongate proliferous leaf tips. Acknowledgment is given to R. Hammer and A. Herndon for bringing these species to my attention.—*Clifton E. Nauman*, Fairchild Tropical Garden, 10901 Old Cutler Road, Miami, Florida 33156.

Review

"*Encyclopaedia of Ferns*," by David L. Jones. 1987. xvii + 433 pp., 251 color plates, 154 b/w illustrations, 78 line drawings. Timber Press, 9999 S.W. Wilshire, Portland, Oregon 97225. $50.00 ISBN 0 88192 054 1.

This most attractive book with its many excellent photographs and drawings is written primarily for fern growers. However, with the need to maintain live plants for research and to save through botanical gardens the rare and endangered species, this book should have an even wider appeal. Part one, the Introduction, Structure and Botany of Ferns, takes about one fourth of the book. It includes a very informative chapter on the economic importance of ferns, with a list of the ferns that are eaten in Asia and the Pacific areas. The chapter on structure is well illustrated for clarity. Under the discussion of root types, fleshy fern roots were not mentioned. Under stipes, the significance of different tissue patterns as seen in cross-sections might have been included. Classifications and life cycles

of pteridophyte orders and some families are discussed in detail. Save for Aspidiaceae, families to which commonly known ferns belong are regretfully omitted. Life cycle details are easily accessible in botany texts, but descriptions of common fern families are not; it seems that an opportunity has been missed in omitting them.

The next quarter of the book deals with the culture of ferns on a how-to-do basis. General and specialized propagation practices, pest and disease control, and hybridization are thoroughly covered, clearly written, and amply illustrated. A number of the horticultural materials suggested for use such as marl, brown coal, basic slag, and blisters, will be unfamiliar or difficult to obtain in the United States, while materials successfully used in the United States such as diazinon for fungus gnats and metalaxyl (Subdue) for root rot are not mentioned and perhaps not available in Australia.

The remaining half of the book lists approximately 700 species of ferns, each followed by a short text. Some species are arranged by taxonomic relationships, some by similarities in growth habit, and some by similarities in cultural requirement. This unusual arrangement necessitates a catch-all category entitled "Miscellaneous ferns." The text after each species gives the common name, synonyms, country of origin, frond dimensions and division, hardiness, habit, and brief comments on cultural needs and uses. Because the descriptions are brief and only select ferns are illustrated, identification of unknown ferns will be mainly incidental. Some of the drawings could have had more diagnostic value if they were less reduced in printing, and some could have been edited with a more critical eye, as in places where peltate indusia should be reniform or vice versa. Emphasis is given to semi-hardy and warmer-climate species in the photographs and illustrations; however, hardier species are covered adequately in the text. Some of the species listed as hardy probably would not survive in the colder parts of the United States and northern Europe. Though one is tempted to mention the genera and species omitted, I am more impressed by the inclusion of so many diverse species. The latest name changes for a number of species have been used with cross-references to most of the well known synonyms. With such a large number of entries it is inevitable some misplacements will appear, such as cultivars under improper species or names under improper pictures. The book concludes with a list of ferns for various landscape purposes, a glossary, bibliography, and list of fern societies and study groups.

The problems I have pointed out are mostly small in comparison to the scope of this book. The many high quality photographs and the thorough and detailed discussion with a hands-on-approach to growing ferns will inspire advanced fern growers to pursue their hobby even more avidly, and will serve to introduce beginning growers to the fascinating world of ferns.—BARBARA JOE HOSHIZAKI, Mildred Mathias Botanical Garden, University of California, Los Angeles, California 90024.

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Referees, 1987

I thank the Associate Editors and referees listed below for their valuable assistance in the review process. Their evaluations of manuscripts submitted to American Fern Journal have aided authors, made my job easier, and contributed to the quality of our journal.—ALAN R. SMITH

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American Fern Journal 78(1): 1–5 (1988)

Ceradenia, a New Genus of Grammitidaceae

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William J. Hooker's generic concepts for ferns essentially dominated the taxonomic community for the latter half of the nineteenth century. We now see that his genera, based almost solely on soral and venational characters, were nearly as artificial in conception as those of Linnaeus' sexual system for flowering plants. With the recognition in this century that some superficially similar groups such as the thelypterids and dryopterids were not at all closely related, the Hookerian dream of easy and obvious fern genera was permanently undermined. Today, even in complex groups, there is still resistance to the elucidation of genera based on nontraditional characters. Although conservatism is generally a cardinal virtue in taxonomy, the maintenance of very large, complex genera seems cumbersome for cases in which natural and discrete groupings of more manageable size can be demonstrated and defined by multiple, correlating characters.

In my paper on *Cochlidium* (Bishop, 1978), I suggested that the only rational alternative to recognizing radically revised generic concepts in the Grammitidaceae is the inclusion of all species of the family into a single genus. Workers in at least two subsequent publications have adopted this approach for New World species (Tryon & Tryon, 1982; Proctor, 1985). The necessarily detailed studies to support more workable and hierarchic generic concepts in the family have proceeded rather slowly. But both Parris, from her studies of Indo-Malaysian species, and I, in my investigation of Neotropical groups, have become convinced that well defined, natural genera can be delimited among these ferns (Parris, 1984, 1986). As to the ease of generic recognition, those who wish to constitute the entire family Grammitidaceae as a single genus are recognizing a genus based on spore and sporangial characters, whereas the natural groupings within the family are to be founded on the more easily observed features of trichomes and general morphology.

Among the larger grammitid ferns, the presence or absence of hydathodes seems to be a conservative character. In the Neotropics, the great majority of anhydathodous species probably constitute an allied group. The only Neotropical anhydathodous grammitids not part of this greater alliance are *Grammitis graminea*, *G. turquina*, and those few species of *Grammitis* sensu stricto in which the hydathodes are reduced to the point of extinction. In addition to lacking hydathodes, ferns of the alliance in question have concolorous scales, generally coriaceous fronds, and rather weak laminar setae. Another interesting character found among these ferns is the tendency for the base of the rachis or the distal stipe to be geniculate. This character is found among the hydathodous grammitids only in *Grammitis asplenifolia* and its immediate relatives.

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This anhydathodous alliance falls quite distinctly into three natural groups. *Glyphotaenium* and another small but striking species group related to *G. mathewsii* are being dealt with elsewhere, while the third is here described as the new genus *Ceradenia*. This genus is most easily characterized by the glanduliferous receptacular paraphyses. Each paraphysis consists of a uniseriate unbranched hair of which the distal 2–5 cells bear globose or obpyriform, waxy glands. These glands are conspicuously white in most species, but in a few they are tan or yellowish. Although the genus name is derived from the waxy appearance of these glands, the actual chemical identity of the substance is unknown. In young sori the glands completely cover the developing sporangia and can be quite apparent even to the unaided eye. In fact, they have been noted in the protologue descriptions of several species, but no author has mentioned them in connection with species other than his own. Among old sori the glands lose their opacity and are rather difficult to detect except with microscopic mountings. In addition, it should be noted that field preservation of specimens in fluid and, possibly, high heat in drying also cause the glands to become clear. With moderate magnification and careful observation, however, the paraphyses will be quite evident in younger sori, even though they will not be strikingly white. Apart from the paraphyses, *Ceradenia* differs from *Glyphotaenium* in lacking setae conspicuously disposed around the sorus. Most species of *Glyphotaenium* show such circum-soral setae, and while no *Ceradenia* has these, a single rather rare species does have receptacular setae, so that this differentiation must be made.

Ceradenia is a rather large genus, comprising about 55 species. Approximately two dozen species await description, but at this time I merely transfer those epithets which I have found to represent valid described species. The species fall quite clearly into two groups, here ranked as subgenera, that differ primarily in the rhizome organization. Although this difference is based on the internal symmetry of the rhizome, with care and some experience this distinction can be discerned by external examination of the stipe insertions. Subgenus *Ceradenia* is characterized by a radically symmetrical rhizome. All but one species bear waxy-glandular laminar trichomes and the stipe is short or lacking. Subgenus *Filicipecten* shows a dorsiventrally organized rhizome. The lamina lacks waxy-glandular trichomes and the stipe is generally 0.5–3 times as long as the lamina. These two subgenera more or less correspond to the groups of *Ctenopteris curvata* and *C. meridensis* of Copeland (1955). However, he included in these groups various species that are not *Ceradeniae* (or even Grammitidaceae), and other species of *Ceradenia* are scattered through his other groupings.

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Ceradenia L. E. Bishop, gen. nov. (Fig. 1)—Type: *Polypodium curvatum* Sw.

Hinc turma major filicum neotropicalium cogitur quarum aliquot vulgariores multae rarae sunt. Rhizoma breve (per unam speciem elongatum) interne siphonostelam amphiphloicam endoderme interna praebens, externe paleis concoloribus integris aut ciliatis nitentibus vel subnitentibus ex cellulis inflatis vel subinflatis constantibus, radialiter aut dorsiventraliter componitur. Lamina

FIG. 1. Exemplary species of *Ceradenia*. Subgenus *Ceradenia*, A–D. A. *C. jungermannioides*. B. *C. pruinosa*. D. *C. discolor*. D. *C. curvata*. Subgenus *Filicipecten*, E–G. E. *C. semiadnata*, portion of frond. F. *C. brunneoviridis*. G. *C. kalbreyeri*.

plerumque pinnatifida pinnatave praeter modum simplex aut bipinnata, setas (pilos simplices quorum muri cellulares secondarie spissantur) pilos hyalinos simplices vel ramosos et/aut pilos glandulosos paraphysum similes gerens, venis maximam partem 1-furcatis nonnunquam simplicibus ordinatim liberis etsi per occasionem conjungentibus, hydathodis caret. Sori mediales vel submarginales ad venulam acroscopicam siti setis circum soros carentes, sporangia capsulis 140–250 × 120–185 μm annulis suis ex 9–13 cellulis constantibus, sporas hemisphaericas vel subtetraedricas frequenter binucleatas 25–55 μm in diametro longiore includentia, etiam paraphyses quarum consistit unaquaeque ex pilo longo cellularum hyalinarum quarum 2–5 distalis glandulis globosis vel obovoideis opacis niveis vel eburneis gerunt, praeterea per unam speciem setas pro paraphysibus continent. Chromosomata $n=37$ per illam speciem solam pro qua numerus decretus est.

Subgenus *Ceradenia*

Rhizome radially symmetrical, with overlapping leaf gaps (dictyostelic); lamina bearing waxy-glandular trichomes, these similar to the paraphyses, but without the long hyaline stalk (no glandular laminar hairs in *C. jungermannioides*); stipe lacking or, if present, less than half the length of the lamina; spores 25–40 μm.

Ceradenia albidula (Baker) L. E. Bishop, comb. nov.—*Polypodium albidulum* Baker in Martius, Fl. bras. 1, 2:598. 1870.

Ceradenia capillaris (Desv.) L. E. Bishop, comb. nov.—*Polypodium capillare* Desv., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 5:316. 1811.

Ceradenia curvata (Sw.) L. E. Bishop, comb. nov.—*Polypodium curvatum* Sw., J. Bot. (Schrader) 1800, 2:24. 1801.

Ceradenia discolor (Hook.) L. E. Bishop, comb. nov.—*Polypodium discolor* Hook., Icon. pl. 4:pl. 386. 1841.

Ceradenia farinosa (Hook.) L. E. Bishop, comb. nov.—*Polypodium farinosum* Hook., Icon. pl. 10:pl. 947. 1854.

Ceradenia fragillima (Copel.) L. E. Bishop, comb. nov.—*Ctenopteris fragillima* Copel., Philipp. J. Sci. 84:470. 1955 [1956].

Ceradenia fucoides (Christ) L. E. Bishop, comb. nov.—*Polypodium fucoides* Christ, Bull. Herb. Boissier II, 5:2. 1905.

Ceradenia herrerae (Copel.) L. E. Bishop, comb. nov.—*Ctenopteris hererae* Copel., Philipp. J. Sci. 84:467. 1955 [1956].

Ceradenia jungermannioides (Klotzsch) L. E. Bishop, comb. nov.—*Polypodium jungermannioides* Klotzsch, Linnaea 20:373. 1847.

Ceradenia nubigena (Maxon) L. E. Bishop, comb. nov.—*Polypodium nubigenum* Maxon, Contr. U.S. Natl. Herb. 17:599. 1916.

Ceradenia pearcei (Baker) L. E. Bishop, comb. nov.—*Polypodium pearcei* Baker in Hook. & Baker, Syn. fil. 508. 1874.

Ceradenia pilipes (Hook.) L. E. Bishop, comb. nov.—*Polypodium pilipes* Hook., Icon. pl. 3:pl. 221. 1840.

Ceradenia podocarpa (Maxon) L. E. Bishop, comb. nov.—*Polypodium podocarpum* Maxon, Smithsonian Misc. Collect. 56, 24:2. 1911.

Ceradenia pruinosa (Maxon) L. E. Bishop, comb. nov.—*Polypodium pruinosum* Maxon, Proc. Biol. Soc. Wash. 52:117. 1939.

Subgenus **Filicipecten** L. E. Bishop, subgen. nov.—Type: *Polypodium kalbreyeri* Baker – 26610047

Rhizome dorsiventrale, solenostelicum; lamina glandulis albidis carens; stipes lamina 0.5–3plo longior; sporae 35–55 μm.

Ceradenia brunneoviridis (Baker ex Jenman) L. E. Bishop, comb. nov.—*Polypodium brunneoviride* Baker ex Jenman (as *P. brunneo-viride*), J. Bot. 15:265. 1877.

Ceradenia fendleri (Copel.) L. E. Bishop, comb. nov.—*Ctenopteris fendleri* Copel. Philipp. J. Sci. 84:463. 1955 [1956].

Ceradenia kalbreyeri (Baker) L. E. Bishop, comb. nov.—*Polypodium kalbreyeri* Baker in Thurn, Timehri 5:215. 1886.

Ceradenia knightii (Copel.) L. E. Bishop, comb. nov.—*Ctenopteris knightii* Copel., Philipp. J. Sci. 84:419. 1955 [1956].

Ceradenia kookenamae (Jenman) L. E. Bishop, comb. nov.—*Polypodium kookenamae* Jenman in Thurn, Timehri 5:215. 1886.

Ceradenia longipinnata (Copel.) L. E. Bishop, comb. nov.—*Ctenopteris longipinnata* Copel., Philipp. J. Sci. 84:459. 1955 [1956].

Ceradenia margaritata (A. R. Smith) L. E. Bishop, comb. nov.—*Grammitis margaritata* A. R. Smith, Proc. Calif. Acad. Sci.40:221. 1975.

Ceradenia mayoris (Rosenstock) L. E. Bishop, comb. nov.—*Polypodium mayoris* Rosenstock, Mém. Soc. Sci. Nat. Neuchâtel 5, 2:53. 1914.

Ceradenia melanopus (Grev. & Hook.) L. E. Bishop, comb. nov.—*Polypodium melanopus* Grev. & Hook. (as *P. melanopum*), Bot. Misc. 3:384. 1833.

Ceradenia meridensis (Klotzsch) L. E. Bishop, comb. nov.—*Polypodium meridense* Klotzsch, Linnaea 20:380. 1847.

Ceradenia nudicarpa (Copel.) L. E. Bishop, comb. nov.—*Ctenopteris nudicarpa* Copel., Philipp. J. Sci. 84:462. 1955 [1956].

Ceradenia semiadnata (Hook.) L. E. Bishop, comb. nov.—*Polypodium semiadnatum* Hook., Icon. pl. 10:pl. 948. 1854.

Ceradenia spixiana (C. Martius ex Mett.) L. E. Bishop, comb. nov.—*Polypodium spixianum* C. Martius ex Mett., Abh. Senckenberg. Naturf. Ges. 2:57. 1856.

Literature Cited

Bishop, L. E. 1978. Revision of the genus *Cochlidium* (Grammitidaceae). Amer. Fern J. 68:76–94.

Copeland, E. B. 1955 [1956]. *Ctenopteris* in America. Philipp. J. Sci. 84:381–471.

Parris, B. S. 1984. Another intergeneric hybrid in Grammitidaceae: *Ctenopteris longiceps* × *Grammitis sumatrana*. Fern Gaz. 12:337–340.

———. 1986. Grammitidaceae of peninsular Malaysia and Singapore. Kew Bull. 41:491–517.

Proctor, G. R. 1985. *Ferns of Jamaica*. London: British Museum [Natural History].

Tryon, R. M. and A. F. Tryon. 1982. *Ferns and allied plants, with special reference to tropical America*. New York: Springer-Verlag.

American Fern Journal 78(1): 6–13 (1988)

Isoëtes ×*hickeyi*: A Naturally Occurring Hybrid between *I. echinospora* and *I. macrospora*

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Speculation about the occurrence of interspecific hybrids in *Isoëtes* began as early as 1896 when Dodge noted that some New England species of *Isoëtes* "intergrade at times." Jeffrey and Hicks (1925) and Jeffrey (1937) attributed variation in size and shape of megaspores, lack of protoplasmic content in microspores, and lagging chromosomes during microsporogenesis to hybridization in *Isoëtes* from Nova Scotia. Boom (1980) artificially crossed several *Isoëtes* species. Subsequently, he proposed six interspecific hybrids from southeastern United States (Boom, 1982). However, Kott and Britton (1983) believed that there was insufficient evidence to support interspecific hybridization in northeastern North American *Isoëtes*, and that either ethological or sterility barriers exist among most taxa. Data are presented here to document the natural occurrence of an interspecific hybrid in *Isoëtes*.

Hybrids between *Isoëtes echinospora* and *I. macrospora* were discovered in Neva Lake, Langlade County, Wisconsin. These plants possess megaspores that are more variable in size, shape, and surface ornamentation than typical megaspores of *I. echinospora* and *I. macrospora*. The origin of *I. echinospora* × *macrospora* is supported by evidence from spore morphology and viability, chromosome counts made from root tip squashes, and electrophoresis of leaf enzymes.

Isoëtes ×**hickeyi** W. Taylor & N. Luebke, hyb. nov.—Type: Wisconsin, Langlade County, Neva Lake, 15 Oct 1983, *Taylor 5010b* (MIL).

Plantae inter *I. echinosporum* et *I. macrosporum* interpositae. Megasporae forma et amplitudine variabiles, plerumque normales hemisphaerio proximali angulari, aliquando globosae hemisphaericae seu libramentiformae, ad 1000 μm longae, ornamento paginae echinato seu reticulato. Microsporae plerumque aprotoplasmicae. Chromosomatum numerus $2n = 66$.

Known only from the type locality, from several collections. Eight plants of *I.* ×*hickeyi (Taylor & Luebke 5157)* are in culture at MIL and will be distributed to herbaria. One plant is at BM. The epithet for this hybrid honors Dr. R. James Hickey, who has encouraged and assisted us in our study of *Isoëtes* in North America.

Materials and Methods

Spore morphology.—Megasporangia of *I.* ×*hickeyi* were opened and their contents dispersed in petri dishes containing demineralized water. Megaspores were examined and photographed through a dissecting microscope. Fifty

megaspores of *I.* ×*hickeyi* and twenty-five megaspores each of *I. echinospora* and *I. macrospora* were air-dried and placed in concavity slides; their greatest diameters, including ornamentation, were measured using a compound microscope fitted with an ocular micrometer. Spore surfaces of *I.* ×*hickeyi*, *I. echinospora*, and *I. macrospora* were examined using an Hitachi S-570 scanning electron microscope (SEM). Air dried spores were mounted on copper tape that had been glued to stubs with colloidal graphite. Mounts were sputter coated with 140 nm of gold. Megaspores were photographed at 100× and microspores at 1000×.

Hydrated microspores of *I.* ×*hickeyi*, *I. echinospora*, and *I. macrospora* were mounted on slides in Aqua-Mount (American Scientific Products). Two hundred twenty-five randomly selected microspores of *I.* ×*hickeyi* were examined for the presence of an ellipsoid endosporium and protoplasm. Ellipsoid endosporia, filled with protoplasm, were measured across their longest diameters in twenty-five microspores each of *I.* ×*hickeyi*, *I. echinospora*, and *I. macrospora*.

Spore viability.—Megaspores of *I.* ×*hickeyi*, *I. echinospora*, and *I. macrospora* were cultured following the procedures described by Taylor and Luebke (1986) for germinating spores of aquatic *Isoëtes*. Three replicate cultures of *I. echinospora* and *I. macrospora* and eight replicate cultures of *I.* ×*hickeyi* were made. Each culture dish contained 30 or more megaspores. After vernalization at 2°C for 100 days, spores were incubated at 18°C with a 12L:12D photoperiod. Cultures were scored for germination after 100 days of incubation.

Chromosome counts.—Chromosome counts of *I.* ×*hickeyi* were made from root tip squashes. Roots up to 1 cm long with white apices were collected between 8 and 9 AM and pretreated for 3 hours in a saturated solution of paradichlorobenzene in the dark at ca 20°C, then fixed in a 3:1 solution of 95% ethanol and glacial acetic acid. Following a protocol similar to that of Wiley (1971, p. 59), each root was hydrolyzed for 30 minutes in a 3:1 solution of 95% ethanol and concentrated HCl, neutralized for 30 minutes in 95% ethanol, stained for 35 minutes in Wittman's hematoxylin, and destained for 3 minutes in glacial acetic acid. Finally, the apical 0.5 mm was removed and placed in a drop of Hoyer's medium where it was macerated with a brass rod and squashed. Chromosome figures were photographed at 1000×.

Electrophoresis.—Leaves from three plants each of *I. echinospora*, *I.* ×*hickeyi*, and *I. macrospora* from Neva Lake were crushed and ground in a buffer solution. The resulting mixtures were absorbed onto filter paper wicks and subjected to horizontal starch gel electrophoresis. Gels were stained for phosphoglucomutase (PGM) and triosephosphate isomerase (TPI). Electrophoretic procedures and composition of grinding buffers, gel and electrode buffers, and staining methods follow Soltis et al. (1983). Phosphate grinding buffer was used for PGM, and Tris-HCl grinding buffer was used for TPI. PGM was resolved on electrode and gel buffer system 5 in a 12% gel and TPI on system 7 in a 13% gel. Electrophoresis was conducted at 4°C and at a constant current of 40 mamp for PGM and 35 mamp for TPI. Wicks were removed from the gels after 15 minutes. PGM was run for 6.5 hrs. and TPI for 8.5 hrs. Gel slices were

incubated in substrates in the dark at 37°C for 1 hr., rinsed in distilled water, and photographed.

Results

Spore morphology.—Megaspores of *I. echinospora* and *I. macrospora* megaspores are typically globose and uniform in size but those of *I.* ×*hickeyi* are variable in shape and size. Most megaspores of *I.* ×*hickeyi* have a flattened, angular proximal hemisphere, others are subglobose to nearly hemispherical, whereas a few appear as tiny wedges or large dumbbell-shaped structures (Fig. 1). Megaspores of *I.* ×*hickeyi* average 465 ± 126 μm across but range from less than 100 μm to over 1 mm in length. Megaspores of Neva Lake *I. echinospora* average 435 ± 26 μm in diameter, ranging from 390 μm to 490 μm, whereas those of Neva Lake *I. macrospora* average 630 ± 47 μm in diameter, ranging from 550 μm to 720 μm.

Differences between the microspores of *I.* ×*hickeyi* and those of *I. echinospora* and *I. macrospora* are seen in the contents and the shape of the enclosing endosporium located within the perine (Fig. 2). Whereas the endosporium of *I.* ×*hickeyi* microspores is variable in shape, often shriveled, and usually contains little or no protoplasm (Fig. 2a), the endosporium of *I. echinospora* and *I. macrospora* microspores is ellipsoid and filled with protoplasm (Figs. 2b, c). Only about 10% of *I.* ×*hickeyi* microspores possess an ellipsoid endosporium and only about one half of these contain any protoplasm (see microspore at lower left in Fig. 2a). Ellipsoid endosporia of *I.* ×*hickeyi* microspores average 34 μm in length, intermediate between those of its putative parents, *I. echinospora* and *I. macrospora*, which average 26 μm and 41 μm in length, respectively.

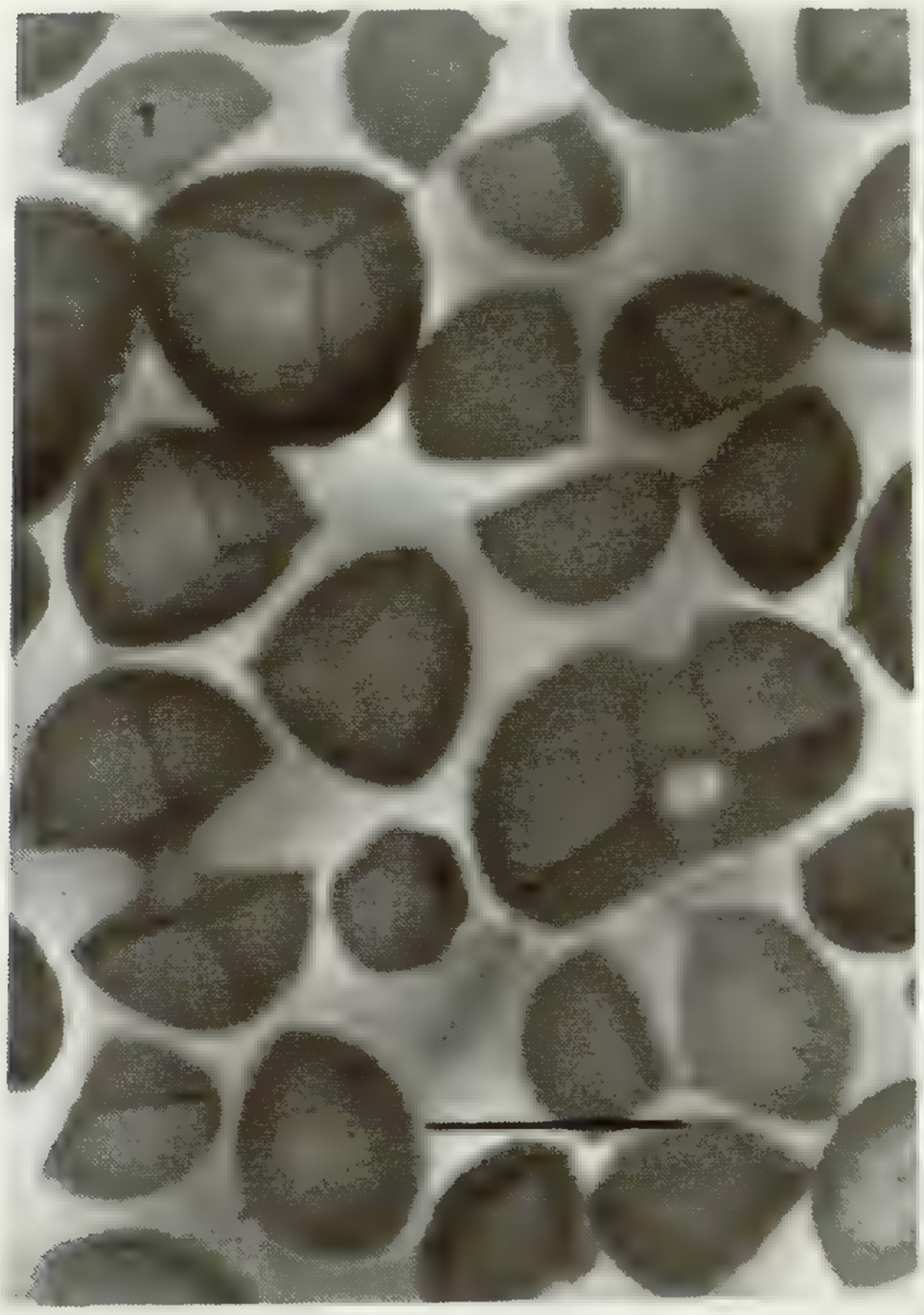
Megaspore ornamentation of *I.* ×*hickeyi* appears to combine ornamentation patterns of both *I. echinospora* and *I macrospora* (Fig. 4). Megaspores of *I. echinospora* are echinate (Fig. 4a), whereas those of *I. macrospora* bear branched to anastomosing ridges and a band of papillae encircling the distal side of the equitorial ridge (Fig. 4b) (Kott & Britton, 1983). Megaspores of *I.* ×*hickeyi* bear spines and short ridges that occasionally branch and anastomose (Figs. 4c, d). They also possess a band of papillae along the distal side of the equatorial ridge.

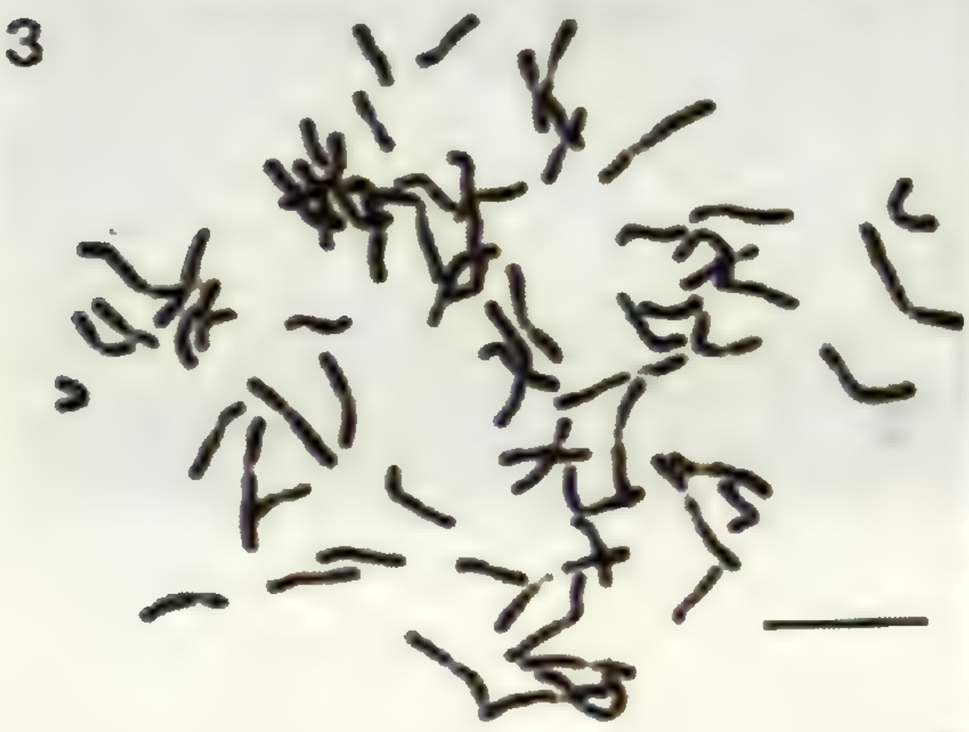
Mature microspores of *I. echinospora* are spinulose (Fig. 5a) and those of *I. macrospora* are papillate (Fig. 5b). Surface ornamentation of *I.* ×*hickeyi* microspores varies from spinulose to tuberculate (Figs. 5c, d).

Spore viability.—Megaspores of *I.* ×*hickeyi* did not germinate in culture, whereas *I. echinospora* and *I. macrospora* megaspores did germinate to form megagametophytes (Table 1). Megaspores were scored as having germinated if they opened to expose gametophytic tissue that developed archegonia.

Chromosome counts.—Root tip cells of *I.* ×*hickeyi* are hexaploid ($2n = 6x = 66$) (Fig. 3). *Isoëtes echinospora* is a diploid ($2n = 2x = 22$) and *I. macrospora* is a decaploid ($2n = 10x = 110$) (Kott & Britton, 1980). Neva Lake *I. echinospora* and *I. macrospora* conform to these published counts.

Electrophoresis.—Enzyme banding patterns for PGM and TPI are shown in Figure 6. The PGM zymogram shows four bands of activity (Fig. 6a). *Isoëtes*





FIGS. 1–3. Spores of *Isoëtes* ×*hickeyi* and parents and *I.* ×*hickeyi* chromosomes. FIG. 1. Incident light photomicrograph of *I.* ×*hickeyi* megaspores in water; bar = 500μm. FIG. 2. Brightfield photomicrographs of *Isoëtes* microspores from Neva Lake; a. *I.* ×*hickeyi*; b. *I. echinospora*; c. *I. macrospora*; bar = 50 μm; (e) endosporium; (p) perine. FIG. 3. Brightfield photomicrograph of *I.* ×*hickeyi* chromosomes in root tip squash; bar = 10 μm.

echinospora expresses only the least anodal band. *Isoëtes* ×*hickeyi* also has this band but it does not appear in *I. macrospora*. *Isoëtes macrospora* expresses three, more anodal bands. *Isoëtes* ×*hickeyi* also has these three bands but they do not appear in *Isoëtes echinospora*. The TPI zymogram shows five bands of activity (Fig. 6b). *Isoëtes echinospora* expresses only the most anodal band. *Isoëtes macrospora* has three, less anodal bands. *Isoëtes* ×*hickeyi* expresses five bands. Four of these bands appear to correspond with bands possessed by either *I. echinospora* or *I. macrospora*. *Isoëtes* ×*hickeyi* has an additional band that occurs between the two most anodal bands for each putative parent.

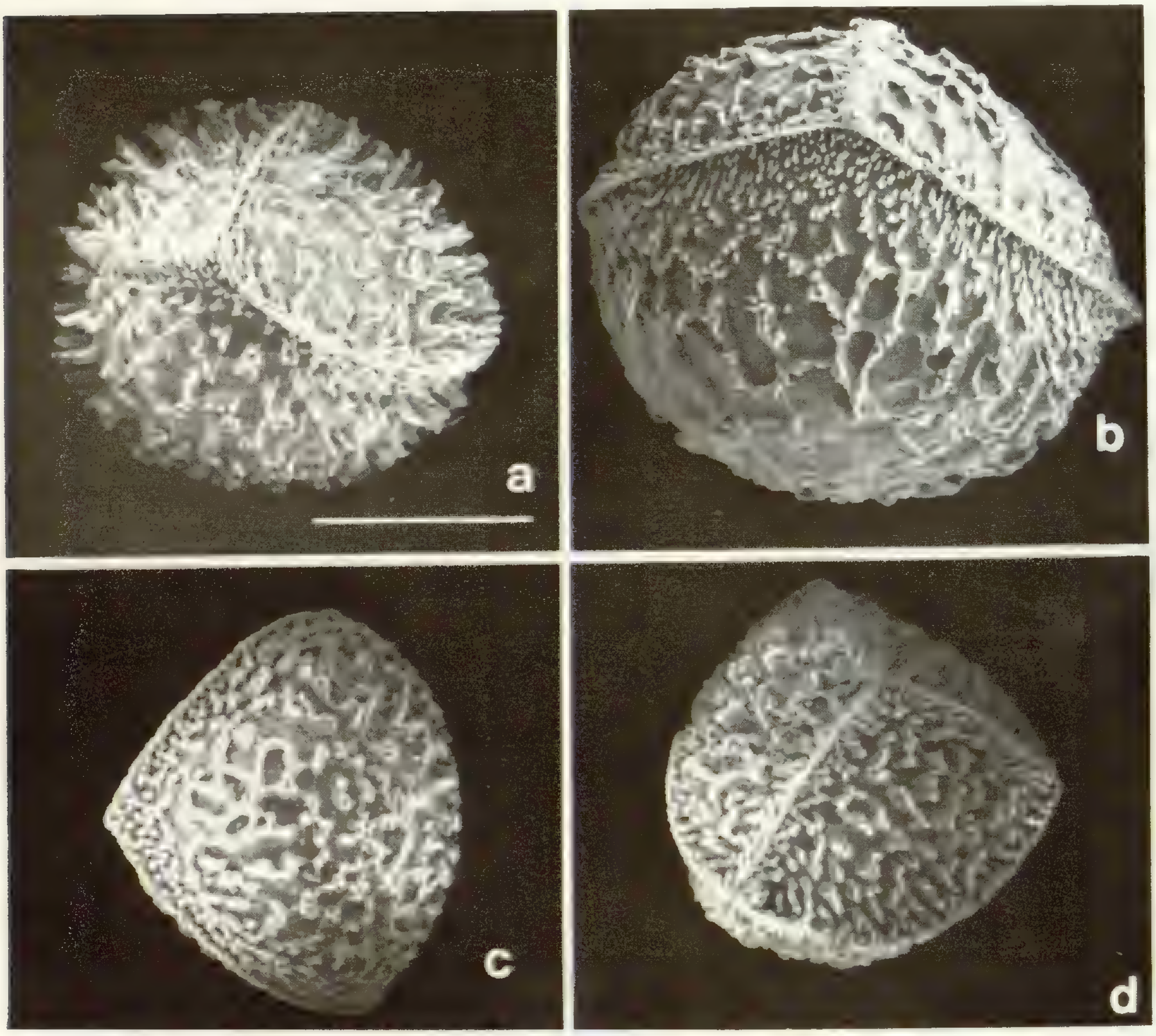


FIG. 4. SEM photomicrographs of *Isoëtes* megaspores from Neva Lake; a. *I. echinospora*; b. *I. macrospora*; c. and d. *I.* ×*hickeyi*; bar = 250 μm.

DISCUSSION

Spore size and ornamentation are often primary characters used to distinguish species of *Isoëtes*. Using a 10× hand lens, it is easy to recognize the globose, echinate megaspores of *I. echinospora* and the ridged to reticulate spores of *I. macrospora*. In contrast, the megaspores of *I.* ×*hickeyi* are often seen as flattened or irregular in form, variable in size, and ornamentated with closely set spines or ridges.

Species of *Isoëtes* produce viable spores which are globose in form and uniform in size. Variable, nonviable spores characterize interspecific hybrids of many pteridophytes (Taylor et al., 1985, Wagner et al., 1986). Megaspores of *I.* ×*hickeyi* are variable in form and size and do not germinate in culture. Microspores of *I.* ×*hickeyi* were not cultured, but a lack of contents indicates most are essentially nonviable.

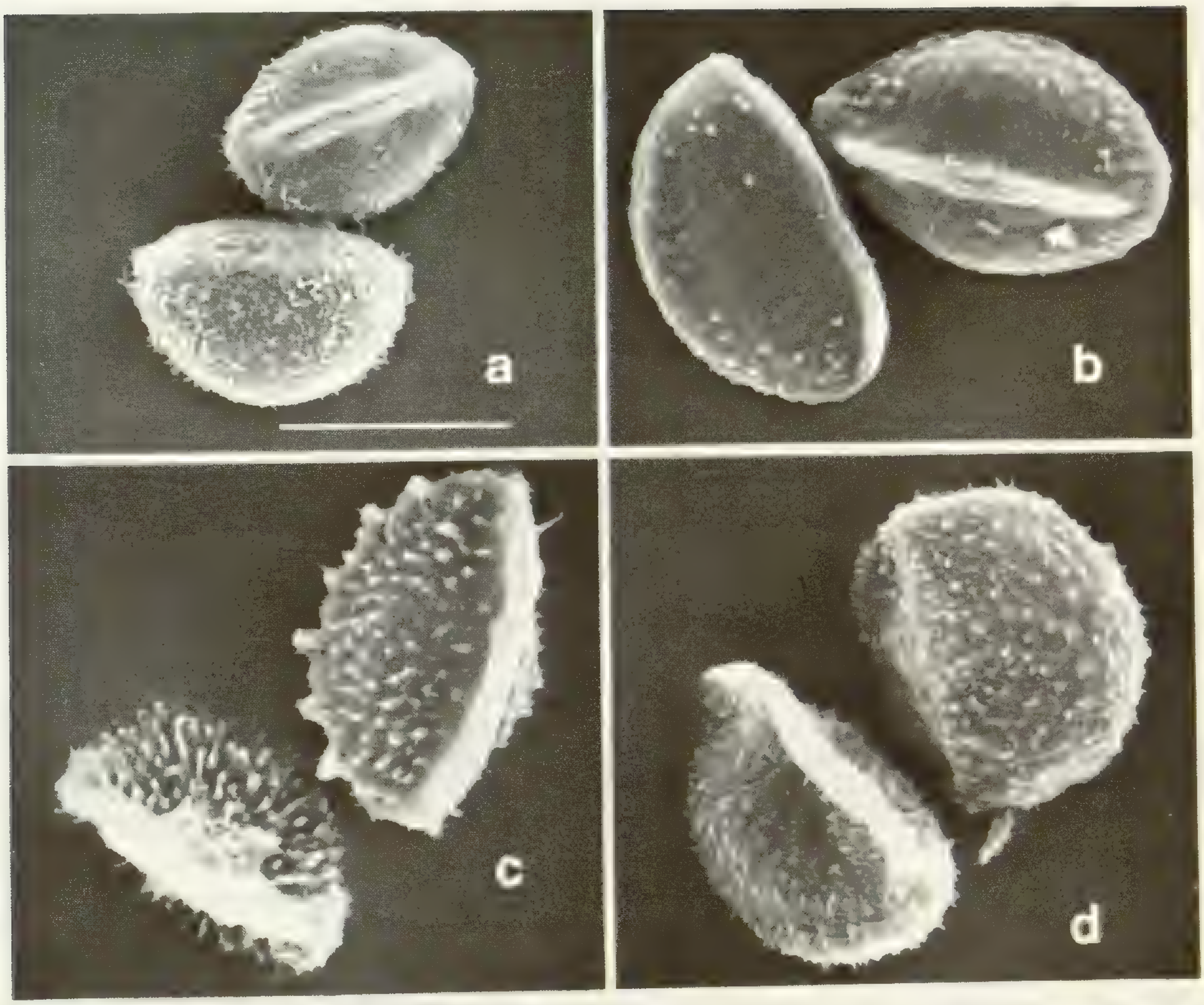


FIG. 5. SEM photomicrographs of *Isoëtes* microspores from Neva Lake; a. *I. echinospora*; b. *I. macrospora*; c. and d. *I.* ×*hickeyi*; bar = 25 μm.

Isoëtes ×*hickeyi* ($2n=66$) has the expected chromosome number for an interspecific hybrid between *I. echinospora* ($2n=22$) and *I. macrospora* ($2n=110$) where their haploid gametes ($n=11$ and $n=55$, respectively) have fused.

Enzyme electrophoretic profiles of *I.* ×*hickeyi* are additive for *I. echinospora* and *I. macrospora* and support the hypothesis of hybrid origin for *I.* ×*hickeyi*.

TABLE 1. In Vitro Megaspore Germination of Neva Lake *Isoëtes* Taxa.

	No. megaspores cultured	No. gametophytes formed	% germination
I. ×*hickeyi*	271	0	0
I. echinospora	90	87	98
I. macrospora	91	91	100

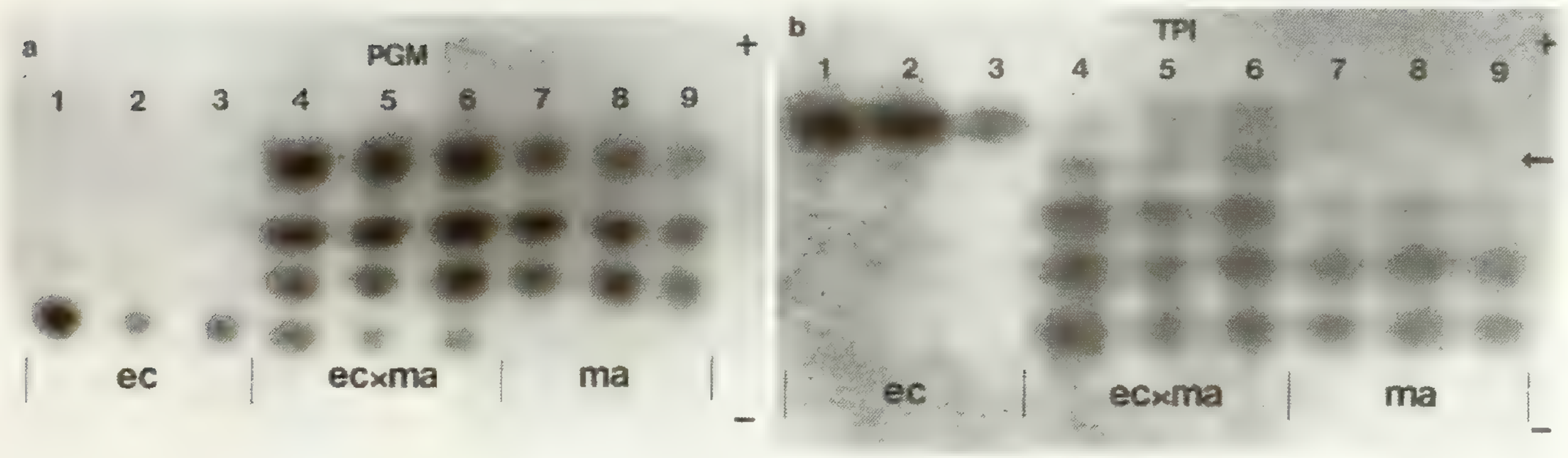


FIG. 6. Starch gels stained for PGM and TPI after electrophoresis of Neva Lake *Isoëtes* leaf enzymes; a. PGM; b. TPI; lanes 1–3 *I. echinospora* (ec), lanes 4–6 *I.* ×*hickeyi* (ec × ma), lanes 7–9 *I. macrospora* (ma). Arrowhead indicates a band that possibly represents a heterodimeric enzyme present only in the hybrid.

Such enzyme characters are valuable in detecting hybrids in pteridophytes (Haufler, 1985). PGM is a monomeric enzyme and TPI is dimeric (Harris & Hopkinson, 1976). The PGM profile for *I.* ×*hickeyi* is additive for all bands expressed by its putative parents. The TPI profile for *I.* ×*hickeyi* is also additive for all bands expressed by its putative parents but it possesses an additional band that probably represents a heterodimeric enzyme formed from subunits coded by genes contributed by each parent. For both PGM and TPI there appears to be fixed heterozygosity in the decaploid, *I. macrospora*. This is not surprising given the high ploidy of this species. From the results obtained, it is impossible to determine with certainty that the bands of enzymatic activity seen on the gels are coded for by alleles at a single locus or by multiple loci.

Dosage effects in *I.* ×*hickeyi* also support the hypothesis of hybrid origin. For both PGM and TPI the bands in *I.* ×*hickeyi* corresponding to those of *I. macrospora* are more intense than those corresponding to *I. echinospora*. This would be expected in a hybrid having five doses of one parent's genes and only a single dose of the other parent's genes.

Data from spore size, shape, ornamentation, and viability in addition to chromosome counts from root tip squashes and electrophoresis profiles of PGM and TPI in leaves indicate that *I.* ×*hickeyi* is a naturally occurring hybrid between *I. echinospora* and *I. macrospora*.

Isoëtes ×*hickeyi* is known only from Neva Lake, a small, glacially formed, soft-water lake with a sand, gravel, and muck bottom. Plants of *I.* ×*hickeyi* were found less than 1 m deep, on the east side of the lake, near a public boat launch. Disturbance from boating, swimming, and wading occurs at the site. *Isoëtes macrospora* is abundant where *I.* ×*hickeyi* was found. Plants of *I. echinospora* are also present at the collection site, but they are more numerous in shallower water, close to shore. *Isoëtes echinospora* and *I. macrospora* are the only species of *Isoëtes* known within a 200 km radius of Neva Lake. Both species are common in the lakes of northern Wisconsin. Their ranges are sympatric over much of eastern North America where they often grow together in the numerous lakes and ponds of this region.

Acknowledgments

We are grateful to David Lellinger for providing us with a Latin description of *I.* ×*hickeyi*. We thank Susan Brahm, Donald Britton, Christopher Haufler, James Hickey, James Montgomery, Clive Jermy, Robbin Moran, Thomas Ranker, Jovanka Ristic, Herb and Florence Wagner, Michael Windham, Charles Werth, and reviewers for their assistance in various ways. We are also grateful to Marilyn Shaller for making the University of Wisconsin-Milwaukee Electron Microscopy Laboratory available to us and to Gretchen Dawes for her kind generosity which made this study possible.

Literature Cited

Boom, B. M. 1980. Intersectional hybrids in *Isoëtes*. Amer. Fern J. 70:1–4.

———.1982. Synopsis of *Isoëtes* in the southeastern United States. Castanea 47:38–59.

Dodge, R. 1896. *The ferns and fern allies of New England*. Binghamton: W. N. Clute & Co.

Kott,L. S. and D. M. Britton. 1980. Chromosome numbers for *Isoëtes* in northeastern North America. Canad. J. Bot. 58:980–984.

——— and ———. 1983. Spore morphology and taxonomy of *Isoëtes* in northeastern North America. Canad. J. Bot. 61:3140–3163.

Harris, H. and D. A. Hopkinson. 1976. *Handbook of enzyme electrophoresis in human genetics*. Amsterdam: North-Holland Publ. Co.

Haufler, C. H. 1985. Pteridophyte evolutionary biology: the electrophoretic approach. Proc. Royal Soc. Edinburgh 86B:315–323.

Jeffrey, E. C. 1937. The cytology of a heterosporous *Isoëtes*. Bot. Mag. (Tokyo)51:203–209.

——— and G. C. Hicks. 1925. The reduction division in relation to mutation in plants and animals. Amer. Naturalist 59:410–426.

Soltis, D. E., C. H. Haufler, D. C. Darrow, and G. J. Gastony. 1983. Starch gel electrophoresis of ferns: A compilation of grinding buffers, gel and electrode buffers, and staining schedules. Amer. Fern J. 73:9–27.

Taylor, W. C. and N. T. Luebke. 1986. Germinating spores and growing sporlings of aquatic *Isoëtes*. Amer. Fern J. 76:21–24.

———, ———, and M. B. Smith. 1985. Speciation and hybridization in North American Quillworts. Proc. Royal Soc. Edinburgh 86B:259–263.

Wagner, W. H. Jr., F. S. Wagner, and W. C. Taylor. 1986. Detecting abortive spores in herbarium specimens of sterile hybrids. Amer. Fern J. 76:129–140.

Wiley, H. L. 1971. *Microtechniques, a laboratory guide*. New York: Macmillan.

excurrent veinlet may even branch and rejoin, forming a narrowly rhombic areola parallel to the main lateral veins.

It is possible that the type of venation found in *C. phyllitidis*, which has rather narrow laminae, is an intermediate stage in the development of the more loosely organized venation found in *C. latum* and in other *Campyloneurum* species with very wide laminae; a succession of fronds on developing plants of *C. latum* should be observed to see if this is true. If so, this may account for the confusion between the two species in Central and South America, where the somewhat inconstant venation has caused some authors to consider the two species to be only one. That decision may prove to be correct, in which case *C. phyllitidis* (all with constant, *phyllitidis*-type venation) ranges from Florida through the Antilles and the Guianas to southern Brazil, and *C. latum* (with both *latum*- and *phyllitidis*-type venation) ranges from Mexico through the Andean countries to Paraguay and Uruguay.

Species with fronds usually less than 4(6) cm wide have branched, areola-forming, slightly or not prominulous main veins usually without transverse veins (*angustifolium*-type venation). The main veins are often sinuous. Because *angustifolium*-type venation is sometimes seen in depauperate fronds of species usually having *latum*-type venation, *angustifolium*-type venation appears to be the basic condition in the genus, and it is reminiscent of other polypod genera like *Microgramma*, which could be ancestral to *Campyloneurum*.

Geography

Campyloneurum is basically neotropical (Fig. 1). Only 3 species are known from North America north of Mexico and only 7 from Paraguay, Uruguay, Chile, and Argentina. More species are known from the Antilles (10), the Guianas and Brazil (19), and Central America (19). The greatest species richness occurs in the Andean countries (27 in Venezuela—Colombia—Ecuador; 27 in Peru and Bolivia). Narrow endemics, those species occurring in a single region of Fig. 1, are most prevalent in Central America (32% of the species) and in Venezuela—Colombia—Ecuador (19% of the species). Wide endemics, those species occurring in two adjacent regions of Fig. 1, are most prevalent in Peru—Bolivia (33% of the species) and in Venezuela—Columbia—Ecuador (30% of the species).

The species as I construe them generally have coherent ranges, which is additional evidence that they are biologically valid entities. Of the ten new species and combinations published in this paper, 4 are narrow endemics (2 from southern Central America and 2 from Brazil), and 4 are wide endemics (2 from the Andean countries, 1 from southeastern Brazil to Paraguay, Uruguay, and northeastern Argentina, and 1 from Costa Rica to Ecuador). Only two species range more widely, *C. irregulare* (Costa Rica; Colombia to Bolivia) and *C. fuscoquamatum* (French Guiana; Colombia to Bolivia).

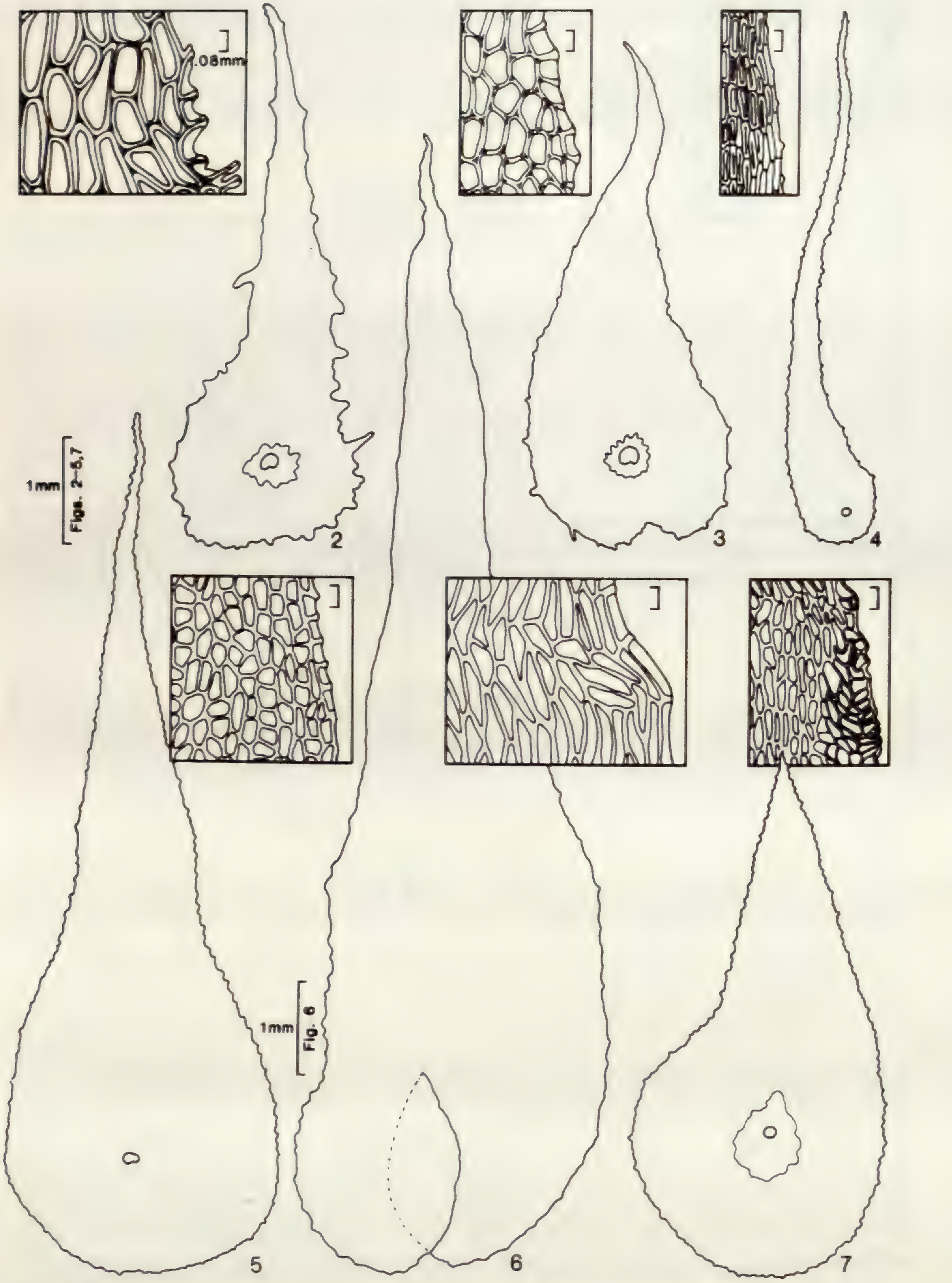
New Species and Combinations

Campyloneurum centrobrasilianum Lellinger, sp. nov. (Figs. 2, 8).—Type: Brazil, Est. Minas Gerais, Viçosa, *Kuhlmann 1898* (US).

FIG. 1. Number of *Campyloneurum* species (and single-region endemics in parentheses) in the various regions of the New World.

Ab *C. angustipaleato* in squamis rhizomatis lanceolatis, subrepandis, ca. 5–8 cellulis latis cellulis sinuatis differt.

Rhizomes short-creeping, 2–2.5 mm in diam., black, not pruinose, the phyllopodia 0.5–1.5 mm long, 1.25 mm in diam.; rhizome scales spreading, concolorous, brown throughout or slightly paler at the margins, lanceolate to rather broadly lanceolate, 2–3 mm long, 0.5–1 mm wide, attentuate at the apex, with overlapping auricles at the base or appearing peltate, the margins repand or rarely with a few short cilia, the cells clathrate with clear, slightly iridescent lumina, those above the base 2–2.5(3) times longer than wide. Stipes 0.5–3 cm long, ca. 1 mm wide, slightly flattened, not sulcate, stramineous. Laminae linear, attenuate at the base and apex, at least slightly revolute at the margins, 12–45(60) cm long, 3–6 mm wide (or sometimes appearing narrower when the margins are



FIGS. 2–7. Rhizome scales of *Campyloneurum* species with cellular detail. FIG. 2. *C. centrobrasilianum*, *Irwin et al. 13057* (US). FIG. 3. *C. cooperi*, *Cooper 6053* (US). FIG. 4. *C. fuscosquamatum*, *Stork & Horton 9452* (US). FIG. 5. *C. inflatum*, *Wurdack 868* (US). FIG. 6. *C. irregulare*, *Holdridge 1577* (US). FIG. 7. *C. wacketii*, *Válio 80* (US).

strongly inrolled due to desiccation), olive green adaxially, paler green with the blackish veins slightly visible abaxially; midrib stramineous or olive green, bearing a few broadly lanceolate, subclathrate, pale brown scales up to 1 mm long and 0.5 mm wide; main lateral veins absent, the veinlets in 1(2) series of areolae with 1 excurrent unbranched fertile veinlet in each areola and marginal free veinlets present; sori ca. 1.5 mm in diam.

Discussion.—This species is closely related to *C. angustipaleatum* (Alston) M. Meyer ex Lellinger and also to other members of the genus with *Vittaria*-like fronds, such as *C. austrobrasilianum* (Alston) de la Sota and *C. aglaolepis* (Alston) de la Sota.

Paratypes: BRAZIL. **Distr. Fed.:** Gallery forest ca. 25 km SW of Brasilia, 1000 m, *Irwin et al. 13057* (F, GH, US). **Goiás**: Gallery forest ca. 30 km N of Alto do Paraiso, ca. 1250 m, *Irwin et al. 33063* (F, UC, US).

Campyloneurum cooperi Lellinger, sp. nov. (Figs. 3, 9).—TYPE: Costa Rica, Pcia. Cartago, Cartago, 4250 ft, *Cooper 6053* (US832717; isotype US829104).

Ab *C. rigido* J. Smith in stipitibus longi brevioribus et squamis rhizomatis cellulis non sinuatis differt.

Rhizomes short-creeping, 4–6 mm in diam., black, slightly pruinose, the phyllopodia 2–3 mm long, 1.5–2 mm in diam.; rhizome scales spreading, concolorous, brown, broadly lanceolate, 2–3 mm long, 1–1.5 mm wide, attenuate at the apex, auriculate with overlapping auricles at the base, the margins entire, the cells clathrate, with translucent, yellowish lumina, those above the base up to 2 times longer than wide. Stipes obsolete or nearly so (up to 1 cm long), ca. 1.5 mm wide, slightly flattened, not sulcate, stramineous or pale brown. Laminae linear, attenuate to a round apex, more gradually attenuate to the base, usually strongly revolute at the margins, 15–50 cm long, 10–16 mm wide, yellowish-green and shiny adaxially, yellowish-green and less shiny with the blackish veins rarely visible abaxially; midrib paler or darker than the lamina surface, bearing a few broadly lanceolate, clathrate, brown scales up to 2 mm long and 1 mm wide; main lateral veins absent, the veinlets in 2 series of areolae with 1 excurrent unbranched fertile veinlet in each areola and marginal free veinlets present; sori ca. 2.5 mm in diam.; receptacular paraphyses and persistent sporangium stalks present.

Discussion.—This very rare species seems to be most closely related to *C. rigidum* J. Smith from southeastern Brazil. Presumably it is a pendent epiphyte. Unfortunately, the locality data are all inexact. Probably it grew on the southern and southeastern slopes of Volcán Irazú, an area now heavily devoted to agriculture. Plants could remain in forests in the Tapantí area. *Campyloneurum cooperi* has been confused with *C. angustifolium*, but has medium brown, rather than dark brown, rhizome scales and especially the basal cells of the scales are isodiametric, rather than distinctly elongate.

Paratype: COSTA RICA. **Cartago**: Turrialba, *Wercklé* in 1901–1905 (US).

Campyloneurum densifolium (Hieron.) Lellinger, comb. nov.—*Polypodium angustifolium* f. *densifolium* Hieron. Bot. Jahrb. Syst. 34:532. 1904, as "*densifolia*."—LECTOTYPE (chosen here): Ecuador, Pcia. Azuay, Cordillera

FIG. 8. Holotype of *C. centrobrasilianum*. FIG. 9. Holotype of *C. cooperi*.

Occidental de Cuenca, near Las Yerbas Buenas, 2500–2900 m, *Lehmann 5723* (US).

Discussion.—Unlike *C. irregulare* Lellinger, with which this species can be confused, *C. densifolium* has mostly or entirely lax, rather adherent rhizome scales that are broadly ovate and peltate at the base, and its rhizomes are not pruinose. These characters also distinguish it from *C. amphostenon*, which has narrow, lanceolate rhizome scales and pruinose rhizomes. Its laminae are regularly 1–3 cm wide (many of them are wider than are those of *C. irregulare*), conspicuous hydathodes are present on the adaxial surface of the laminae, and the plants are usually epipetric or terrestrial, although sometimes they are epiphytic.

Representative specimens: VENEZUELA. **Mérida**: 25 km from Mérida along El Valle road, ca. 2800 m, *Breteler 4663* (US). COLOMBIA. **Magdalena**: Sierra de Perijá, 11 km ENE of Manaure, 47 km E of Valledupar, 2700 m, *Grant 10838* (COL, US). **Norte de Santander**: Road from Pamplona to Toledo, crossing the divide between R. La Teja and R. Mesme, 2800–3000 m, *Killip & Smith 19858* and *19915* (both GH, US). **Santander**: Mountains E of Las Vegas, 3000–3300 m, *Killip & Smith 15809* (GH, US). **Cundinamarca**: Low ridge E of Calle 55, Bogotá, 8800–9000 ft, *Little & Little 7825* (GH, US). **Antioquia**: Páramo de Sonson, ca. 2750 m, *de Garganta F. 2049* (US). **Valle**: E slope of Cordillera Central, basin of R. Bugalagrande, Cuchilla de Barragán between Las Azules and Las Violetas, 3100 m, *Cuatrecasas 20797* (F, US). **Cauca**: Mt. Purace, Canaán, 3100–3300 m, *Killip* (GH, US). **Nariño**: Cordillera Oriental, headwaters of R. Guapuscal above pueblo of Caballo Rucio, 3000 m, *Ewan 16555* (US). ECUADOR. **Carchí**: 18 km W of Julio Andrade on road to El Carmelo, 3200 m, *Boom, Balslev & Luteyn 1402* (US). **Pichincha**: Km. 28 of old Quito–Sto. Domingo road via Chiriboga, 3130 m, *Dodson et al. 10857* (US). **Cotopaxi**: Km. 78 of the Quevedo–Latacunga road, 2750 m, *Dodson et al. 10667* (US). **Tungurahua**: Caserio Runtun, ca. 3–4 km from Baños, *Lugo S. 1222* (GH, UC). **Los Rios**: Road above Balsabamba, 2800 m, *Haught 3299* (US). **Cañar**: Near village of S. Marcos, 5–8 km NE of Azogues, *Camp (Prieto) E–2598* (US); N rim of valley of R. de Cañar between Suscal and Chontamarca, *Camp (Giler) E–2875* (US). **Azuay**: Vic. of the lake in valley of R. Surucuchu (a branch of R. Matadero), 18–20 km W of Cuenca, 9800–10300 ft, *Camp E–4227* (UC, US). **Loxa**: Muletrack between Amaluza and Palanda, W slope of C. Amarillo, 3000 m, *Oellgaard & Balslev 9610* (GH). **Napo**: Papallacta, ca. 3100–3300 m, *Harling et al. 10329* (GH, US). PERU. **Cajamarca**: Las Tres Cruces (Guzmango–Contumaza), 2700 m, *Sagásteguí & Fukushima 5122* (GH). **Amazonas**: Upper slopes of Puma-urcu ESE of Chachapoyas, 2700–3000 m, *Wurdack 706* (US). **S. Martín**: Tarapoto, 750 m, *Ll. Williams 6127* (F). **La Libertad**: Laguna de los Ichus, 3600 m, *Lopez & Sagástegui 3236* (GH). **Lima**: Huaccana, cerro E of Tupe, 2830 m, *Cerrate 1062* (GH). **Junín**: Queros, *Soukup 6170* (GH). **Pasco**: Between Huariaca and C. de Pasco, 3800–3900 m, *Ferreyra 9502* (GH). **Huancavelica**: Yacuhuamay, 6 km below Surcubamba, 2200 m, *Tovar 3680* (GH). **Cuzco**: Chincheros, 3500–3600 m, *Davis et al. 1649* (F). BOLIVIA. **La Paz**: Sorata, *R. S. Williams 2635* (US). **Province unknown**: R. Sanjana, 3200 m, *Herzog 2391* (US).

Campyloneurum fuscosquamatum Lellinger, sp. nov. (Figs. 4, 10).—TYPE: Peru, Depto. Huánuco, Tingo María on the Río Huallaga, *Stork & Horton 9452* (US; isotypes F, GH, UC).

Ab *C. repenti* in squamis rhizomatis longioribus angustioribusque integris concoloribus vel leviter bicoloribus fuscis differt.

Rhizomes very long-creeping, 1.5–2.5 mm in diam., pale green turning tan or blackish in age, not pruinose, the phyllopodia 0–1 mm long, ca. 2 mm in diam., rhizome scales strongly spreading, concolorous or slightly bicolorous, blackish-brown, sometimes paler at the margin, acicular-lanceolate from a dilated base, 3–3.5 mm long, 0.75–1 mm wide at the base, ca. 0.1 mm wide above the base, attenuate at the apex, nearly orbicular with short, non-overlapping

auricles at the base, the margins entire, the cells subclathrate with narrow, almost occluded lumina, those above the base 2–4 times longer than wide. Stipes variable with respect to the lamina length, (1)2–10(18) cm long, 1–2 mm wide, flattened or slightly sulcate, stramineous. Laminae narrowly elliptic to narrowly lanceolate, caudate or occasionally acute at the apex, acute (in broad laminae) to acuminate (in narrow laminae) at the base, plane or scarcely revolute at the cartilaginous margins, 20–40 cm long, 2–8 cm wide, rather dark olive green adaxially, paler olive green abaxially; midrib pale brown or often blackish, bearing a few scales like those of the rhizome except about 1/3 as large; main lateral veins 4–7 mm distant, prominulous; transverse veins flush or within the lamina tissue, more visible from the adaxial than the abaxial side, always bearing 2 fertile included veinlets and lacking an intermediate sterile veinlet; marginal free veinlets absent; sori 1–1.5 mm in diam., paraphyses absent.

Discussion.—This species was formerly confused with *C. repens* (Aublet) C. Presl, largely because both species have a thin, very long-creeping rhizome and because some lamina forms of *C. fuscosquamatum* resemble those of *C. repens*. This species is an epiphyte or perhaps a hemiepiphyte on shrubs and small trees, mostly at low elevations.

Paratypes: COLOMBIA. **Meta:** Sierra de la Macarena, trail between R. Guëjar and Caño Guapayita, ca. 500–600 m, *Idrobo & Schultes 817* (GH, US). **Caquetá**: 20 km SE of Garzón, 7800 ft, *Little 9379* (US). ECUADOR. **Imbabura**: Vic. of Laguna de la Virgen on ridge S of R. Clavadero, E of Cayambe Peak, 8750 ft, *Wiggins 10459* (US). **Pichincha**: Cordillera Occidental, Corazón Peak and Pass, 2800 m, *Ewan 16419* (US). PERU. **S. Martín**: Road to R. Tocache, 400 m, *Schunke V. 3590* (F, UC, US). **Loreto**: Supte River N of Tingo María, 600 m. *Stork & Horton 9568* (F, GH, UC, US). **Junín**: E of Quimiri Bridge near La Merced, 800–1300 m, *Killip & Smith 23896* (F, GH, US). **Ayachucho**: R. Apurimac Valley, near Kimpitiriki, 400 m, *Killip & Smith 22861* (F, US). **Cuzco**: Ca. 4 km NE of Hac. Luisiana and Apurimac River, ca. 670 m, *Dudley 11501* (GH, US). BOLIVIA. **La Paz**: Road to Tipuani, Hac. Simaco, 1400 m, *Buchtien 5257* (GH, US); **Cochabamba**: Antahuacana, 160 km NE of Cochabamba, 750 m, *Buchtien 2154* (UC, US), *2155* (US), and *2158* (GH, US). FRENCH GUIANA. Foot of Mt. Galbao, 10 km W of Saül, *de Granville 8500* (CAY, NY, P, US, Z).

Campyloneurum inflatum M. Meyer ex Lellinger, sp. nov. (Figs. 5, 11).—TYPE: Colombia, Depto. Cauca, Cordillera Occidental, W slope of Cerro de Munchique, basin of R. Tambito, 2000–2500 m, *Arbelaez & Cuatrecasas 6244* (US; isotypes COL not seen, F).

Ab *C. sublucido* in laminis maioribus non lucidis et soris maioribus differt.

Rhizomes long-creeping, 2–2.75 mm in diam., greenish to stramineous but turning black in age, not pruinose, the phyllopodia 1–2 mm long, ca. 3 mm in diam.; rhizome scales dense, spreading, persistent, concolorous or slightly bicolorous, golden turning brown with golden margins in age, lanceolate from a slightly dilated base, 4–5 mm long, 1 mm wide, attenuate at the apex, with overlapping auricles at the base or appearing peltate, the margins bearing low teeth formed by the extension of end walls of adjacent marginal cells, the cells clathrate with translucent, yellowish lumina, those above the base 1–2 times longer than wide. Stipes 3–4 cm distant along the rhizomes, 9–22 cm long, 1.5–2 mm wide, slightly sulcate at least at the apex, stramineous. Laminae elliptical, acuminate to caudate at the apex, acute or subacute at the base, slightly revolute at the broadly cartilaginous margins, 15–31 cm long, 5.5–10.5 cm wide, pale

FIG. 10. Holotype of *C. fuscosquamatum*. FIG. 11. Holotype of *C. inflatum*.

green on both surfaces; midrib stramineous, bearing a few minute scales (less than 1 mm long) like those of the rhizome, with some of the scales reduced almost to hairs; main lateral veins prominulous on both surfaces, more strongly so on the abaxial surface; transverse veins all occult, bearing 2(3) excurrent fertile veinlets, the intermediate sterile excurrent veinlet absent, incomplete, or complete (especially toward the margin of the frond); marginal free veinlets absent; sori ca. 3 mm in diam.; sporangium stalks persistent; paraphyses absent.

Discussion.—This species has been found in high, montane rainforests in southwestern Columbia and northern Peru. It is unusual in having large laminae with the stipes about equalling the laminae in length.

Paratype: PERU. **Amazonas**: 2–4 km WSW of Pomacocha, 2200–2400 m, *Wurdack 868* (US).

Campyloneurum irregulare Lellinger, sp. nov. (Figs. 6, 12).—TYPE: Ecuador, Pcia. Pichincha, vicinity of Quito, 3000 m, *Holdridge 1580* (US).

Ab *C. amphostenone* in squamis rhizomatis cellulis contortis et ab *C. densifolio* in squamis rhizomatis lanceolatis patentibus differt.

Rhizomes rather short-creeping, (2)3–5 mm in diam., usually brown, strongly pruinose, the phyllopodia 1–3 mm long, 2 mm in diam.; rhizome scales dense, spreading, persistent or not, concolorous, medium to dark brown or rarely yellowish, lanceolate from a slightly dilated base, 3–5 mm long, 0.5–1.5 mm wide, attenuate at the apex, with overlapping auricles at the base or appearing peltate, the margins entire, the cells mostly contorted, clathrate with translucent, yellowish lumina, those above the base 1–4 times longer than wide. Stipes 0.25–1 cm distant along the rhizomes, (2)3–15(21) cm long, 1.25–2 mm wide, sulcate, the lamina margins prolonged toward the base of the stipe as narrow alae or lateral sulcae, stramineous. Laminae linear, attenuate at the apex and base, slightly to greatly revolute at the narrowly cartilaginous margins, (6)10–37(50) cm long, (0.5)1–2(3) cm wide, pale green adaxially, slightly paler abaxially, midrib usually stramineous, sometimes pale green, rarely blackish abaxially, bearing a few scales like those of the rhizome but about half as large; main lateral veins if present flexuous, poorly or not developed, the areolae in (1)2–3 series with 1 or 2 series fertile; marginal free veinlets absent or nearly so; hydathodes prominent on the adaxial surface of the laminae; sori 1.5–2.5 mm in diam.; sporangium stalks persistent; paraphyses absent.

Discussion.—This species has a range similar to that of *C. densifolium* (Hieron.) Lellinger, which it also resembles to some extent. The rhizomes of *C. irregulare* are pruinose and bear rather firm, spreading, lanceolate rhizome scales with overlapping auricles; the laminae are often narrower than those of *C. densifolium* and less often have conspicuous hydathodes. The plants are mostly epiphytic, although they may be terrestrial or epipetric, especially at high elevations.

Paratypes: COSTA RICA. **Alajuela**: Hills of Santiago nr. S. Ramón, 1200–1300 m, *Brenes 14209* (GH). **S. José**: S. Jerónimo, 1500 m, *Wercklé 546* (US). **S. José & Cartago**: Along Interamerican Hwy. ca. 15–20 km SE by road from El Empalme, ca. 2600 m, *Lellinger 1172* (US). **Cartago:** Cartago, ca. 4750 ft, *Scamman 6163* (GH). PANAMA. **Chiriquí**: Volcan de Chiriquí ca. 7.3 mi from Boquete, *Armond 533* (F). COLOMBIA. **Magdalena**: SE slopes of Sierra Nevada de Sta. Marta: basin of R. Donachuí: Cancurúa, 2400–2650 m, *Cuatrecasas & Castaneda 24730* (US). **Santander**: Vicinity of Vetas,

FIG. 12. Holotype of *C. irregulare*. FIG. 13. Holotype of *C. wacketii*.

3100–3250 m, *Killip & Smith 17258, 17315, 17900* (all GH, US). **Boyacá**: Sierra Nevada de Cocuy: near R. S. Pablin, ca. 3800 m, *Grubb & Guymer P15a* (US). **Cundinamarca**: Ca. 5 km SW of Bogotá on road to Usme, ca. 2800 m, *Smith & Idrobo 1319* (GH, UC, US). **Cauca**: Alto de Batanes, ca. 2900 m, *Core 892* (US). **Nariño**: Slope of V. Galeras above Pasto, 3300 m, *Correll Co484* (UC, US). ECUADOR. **Carchí:** Vic. of El Angel, 10000–12000 ft, June 1921, *Popenoe* (US). **Imbabura**: Trail SW of Ibarra, 2350 m, *Mexia 7402* (F, UC). **Pichincha**: Between La Magdalena and Chillogallo, 2800 m, *Firmin 454* (US). **Cotopaxi**: First ridge W of Latacunga, 3650 m, *Humbles 6289* (UC). **Tungurahua**: Vic. of Ambato, *Rose 22370* (US). **Chimborazo**: Vic. of Huigra, *Rose 22270* (GH, US). **Loja**: Vic. of Tablón de Oña, *Rose 23114* (US). PERU. **Cajamarca**: Cerro Cumba Mayo, 3100 m, *Sánchez Vega 36* (GH, US). **La Libertad**: Above Cachicadan, 2900 m, *Stork & Horton 9969* (F, UC, US). **Ancash**: Conzuzo, Pampas, 3800 m, *López M. 1158* (US). **Lima**: R. Blanco, ca. 3600 m, *Asplund 11299* (US), 12000 ft, *Macbride & Featherstone 716* (F). **Junín**: Huancayo, 3317 m, *Soukup 3143* (F, GH, US). **Cuzco**: Hills of Saxaihuamán, 3500 m, *Herrera 204* (US), 3600 m, *Herrera 2371* (F). **Puno**: Vic. of Lake Titicaca, Moho, 3125 m, *Shepard 54* (US). BOLIVIA. **La Paz**: Pongo, *Tate 106* (US).

Campyloneurum major (Hieron. ex Hicken) Lellinger, comb. nov.—*Polypodium phyllitidis* f. *major* Hieron. ex Hicken, Rev. Mus. La Plata 15:272. 1908.—SYNTYPES (all Argentina: Pcia. Misiones): Arroyo Ñacanguazú, near Puerto Tamaren, 12 Feb 1883, *Niederlein* (B); Ruins at Candelaria, 20 Feb 1883, *Niederlein* (B); and "Bei der Plantage El Primer Misionero von Hernandez, Puck and Fernandez," *Neiderlein 237* (B).

Discussion.—This species has been confused with *C. phyllitidis*, from which it differs in having distinctly creeping rhizomes, suborbicular to broadly ovate, subappressed rhizome scales, and more complex venation. It is known from southern Brazil (coastal Rio de Janeiro, São Paulo to Rio Grande do Sul), Paraguay, Uruguay, and Argentina. *campyloneurum phyllitidis* is absent from this region, and all specimens so identified are *C. major*.

Representative specimens: BRAZIL. **Rio de Janeiro**: Cabo Frio Island, *Segadas-Vianna et al. "Restinga I" 743* (US). **São Paulo:** Alto da Serra, Biological Station, 800–900 m, *Smith 1891* (US). **Paraná**: Jaguariahyva, *Dusen 10057* (US), *17354* (US). **Sta. Catarina**: Blumenau, *Haerchen [Ros. Fil. Austrobras. Exs. 115]* (US). **Rio Grande do Sul:** Porto Alegre, *Lindman [First Regnell Exped. Fil. A499]* (US). URUGUAY. **Tacuarembó**: Gruta Helechos, *Herter Pl. Urug. 1231 [Herb. Hert. 3739]* (GH, UC, US). PARAGUAY. **Concepción**: Between the R. Apa and the R. Aquidaban, *Fiebrig 5079* (GH, US). **Guaira**: Colonia Independencia, *Lourteig 1980* (US). **Misiones**; Santiago, Estancia "La Soledad," *Pedersen 9548* (UC, US). **Paraguarí**: NE of Cerro Sto. Tomas, near Paraguarí, *Balansa 2884* (US). ARGENTINA. **Corrientes**: Depto. Mburucuya, Estancia "Santa Teresa," *Pedersen 1803* (US). **Misiones**: Depto. S. Ignacio, Salto Tabay, *Crisci 236* (US).

Campyloneurum remotifolium (Hieron.) Lellinger, comb. nov.—*Polypodium angustifolium* f. *remotifolium* Hieron., Bot. Jahrb. Syst. 34:531. 1904, as "*remotifolia.*"—TYPE: Colombia, Depto. Tolima, Mt. Ruiz, 3000 m, May 1882, *Schmidtchen* (B not seen); and Depto. Cauca, Páramo de las Delicias, 3200–3600 m, *Lehmann 4439* (B not seen; isosyntype US).

Discussion.—This species differs from *C. angustifolium* (Swartz) Fée in having fronds about twice as long and with stipes more than twice as long. It is largely restricted to páramos, unlike *C. angustifolium*. In aspect it also resembles *C. amphostenon*, which also grows at high elevations, but is more delicate.

Representative specimens: VENEZUELA. **Mérida**: Sra. de la Culata, W flank of Los Adobes, páramo Los Conejos, 3500–3650 m, *Ruiz-Terán 6998* (US). COLOMBIA. **Valle:** Cordillera Occidental, Los

Farallones, 3500–3600 m, *Cuatrecasas 17969* (GH, US). ECUADOR. **Imbabura**: Lago S. Marcos, Cayambe, 11200 ft, *Cazalet & Pennington 5374* (UC, US). **Pichincha:** Tambillo, 2700 ft, *Mille* in 1918 (US). **Azuay**: N and NW of Páramo del Castillo, ca. 6–8 km NNE of Sevilla de Oro, 10000–11200 ft, *Camp E–5150* (US). **Napo**: C. Cubillán, 3400–3800 m, *Rimbach (Ros. Fil. Ecuad. Exs. 2)* (UC, US). PERU. **Junín**: Km. 129–130 of the Concepción–Satipo road, ca. 10000 ft, *Saunders 1068* (GH). **Ayacucho**: E massif of Cordillera Central opposing the Cordillera Vilcabamba between Tambo S. Miguel, Ayna, and Hacienda Luisiana, ca. 3400–3600 m, *Dudley 12029* (US). **Cuzco**: Tres Cruces, upper edge of Parque Nac. de Manú, 1–13 km NW of Paucartambo–Pilcopata Road, 3330–3500 m, *Gentry et al. 23450* (US). BOLIVIA. **Cochabamba**: Between Llantas and Aduana, 3100 m, *Steinbach 9557* (UC, GH). **Sta. Cruz**: Yungas de S. Mateo, Comarapa, 2000 m, *Steinbach 8442* (GH).

Campyloneurum wacketii Lellinger, sp. nov. (Figs. 7, 13)—TYPE: Brazil, Est. S. Paulo, Rio Grande, *Wacket (Ros. Fil. Austrobras. Exs. 213)* (US; isotypes GH, UC).

Ab *C. brevifolio* (Link) Link et *C. coarctato* (Kunze) Fée in laminis anguste elliptico-oblanceolatis ad basin sensim decrescentibus differt.

Rhizomes long-creeping, blackish, 3–5 mm in diam., the phyllopodia 2–4 mm long, ca. 5 mm in diam.; rhizome scales spreading, weakly bicolorous, somewhat crisped, dark brown with paler margins, lanceolate (the smaller scales broadly so), 1.5–3 mm long, 0.5 mm wide, acute at the apex, peltate at the base, the margins entire or slightly repand, the central cells clathrate, with transparent lumina, those above the base 2–4 times longer than wide, the marginal cells scarcely clathrate, with translucent lumina, often worn away in age. Stipes obsolete (1–3 cm long), 2–4 mm wide, distinctly sulcate adaxially, stramineous. Laminae narrowly elliptic-oblanceolate, acute or acuminate at the apex, attenuate at the base, scarcely revolute at the narrowly cartilaginous margins, 60–90 cm long, (4)5–6.5(7) cm wide, olive-green and dull adaxially, somewhat paler abaxially; midrib olive-stramineous, glaborus and strongly keeled abaxially; main lateral veins slightly flexuous, prominulous on both surfaces; transverse veins subarcuate, subflexuous, not prominulous, regularly with 2 fertile excurrent veinlets, the intermediate sterile veinlet absent, partial, or complete, especially toward the margins of the frond lamina; marginal free veinlets absent; hydathodes minute, often inconspicuous; sori 1–1.5 mm in diam.; sporangium stalks persistent; paraphyses absent.

Discussion.—This species seems closely related to *C. brevifolium* (Link) Link and to *C. coarctatum* (Kunze) Fée in having rather thick rhizomes and laminae that are long-tapered at the base with nearly obsolete stipes. These species differ from *C. phyllitidis* and its allies in having long-creeping rhizomes with somewhat distant stipes. Specifically, the rhizome scales of *C. wacketii* are lanceate and their cells are elongate and very narrow, whereas those of *C. phyllitidis* are ovate and their cells are nearly isodiametric. Their primary transverse veins are arcuate, rather than angular or nearly straight.

Paratypes: BRAZIL. **Rio de Janeiro**: Paineiras, Pedra do Beijo, *Carauta 285* (F). **São Paulo**: Sa. Arariba, *Brade 8443* (UC); Iguape, Morro das Pedras, *Brade* in 1924 (US); Ubatuba, Instituto Oceanográfico, *Válio 80* (US). **Paraná**: Ilha do Mel, *Hatschbach & Guimaraes 256880* (UC). **Sta. Catarina:** Joinville, *Schmalz 13* (F); Antonio Carlos, Biguassu, *Reitz 274* (US); Brusque, Mata Hoffmann, *Reitz 3091* (US); Brusque, Peterstrasse, *Reitz 3166* (US); Itajai, Morro da Ressacada, *Reitz & Klein 2325* (US); Itajai, Luis Alves, *Reitz & Klein 2378* (US); S. Francisco do Sol, Gauiva, Pôrto do Palmital, *Reitz & Klein 5832* (US).

Campyloneurum wercklei (Christ) Lellinger, comb. nov.—*Polypodium wercklei* Christ, Bull. Herb. Boissier, II. 5:7. 1905.—LECTOTYPE (chosen here): Costa Rica, without locality, *Wercklé* (P-Hb. Christ not seen). The other syntype is: Costa Rica, Pcia. S. José, R. Sucio, 800 m, *Lehmann 1741* (B not seen, P-Hb. Christ not seen, US; see discussion below).

Rhizomes very long-creeping, (1)1.5–3 mm in diam., usually greenish, not pruinose, the phyllopodia 1–2 mm long, 2–3 mm wide in diam.; rhizome scales dense, subappressed, often not or only the scale bases persistent, slightly bicolorous, medium brown at the center but slightly paler toward the margins, lanceolate, 1–2 mm long, ca. 0.75 mm wide, subacute to attenuate at the apex, peltate at the base, the margins entire or shallowly toothed, the cells not to slightly contorted, clathrate with mostly yellowish lumina, those above the base 2–3 times longer than wide. Stipes 1–4 cm distant along the rhizomes, 4–18 cm long, (0.75)1–2(2.5) mm wide, slightly sulcate, stramineous or brownish (especially in Ecuadorian specimens). Laminae narrowly elliptic to narrowly lanceolate, acuminate to caudate at the apex, acute to acuminate at the base, the narrow, cartilaginous margins plane or nearly so, 10–26 cm long, 2–7 cm wide, medium green adaxially, paler abaxially; midrib stramineous or pale brown, glabrous; main lateral veins straight or slightly flexuous, prominulous; transverse veins flexuous, sometimes slightly prominulous, with 2 fertile excurrent veinlets in each areola; marginal free veinlets few, short; hydathodes prominent on the adaxial surface of the laminae; sori 1.5–2 mm in diam.; sporangium stalks persistent; paraphyses absent.

Discussion.—This species was formerly confused with *C. sphenodes* (Kunze) Fée, which I believe is restricted to northeastern Colombia and Venezuela. It differs from *C. sphenodes* and from *C. macrosorum* Fée in having appressed, subdeciduous rhizome scales and thinner, greenish rhizomes. The Ecuadorian specimens, which are disjunct from the Central American ones, differ slightly in having generally larger (or at least wider) laminae and rhizome scales that are more strongly toothed. It is possible that they represent a separate subspecies.

Lehmann 1741 was thought by Christ to be sterile material of *Polypodium wercklei*, which it clearly is not, and so it should not be chosen lectotype of this species. In order to fix the application of this name and of *P. falcoideum* Kuhn ex Hieron., I choose *Lehmann 1741* (US; isolectotypes B not seen, P not seen) as lectotype of the latter species.

Representative specimens: COSTA RICA. **Guanacaste**: Los Ayotes near Tilarán, 600–700 m, *Standley & Valerio 45407* (US). **Puntarenas**: 1–4 km SW of biological field station at Finca Wilson, 5 km S of S. Vito de Java, 1200–1400 m, *Mickel 3122* (US). **Alajuela**: NW of Zarcero, ca. 2 km W of Zapote on road to Sta. Elena, ca. 1200 m, *Lellinger 1357* (CR, F, MO, US). **Heredia**: Yerba Buena, NE of S. Isidro, ca. 2000 m, *Standley & Valerio 49225, 50227, 50251* (all US). **S. José**: La Palma, 1459 m, *Tonduz 12609* (US), 1550 m, *Tonduz 12424* (US). **Cartago**: El Muñeco, 5000 ft, *Stork 2670* (UC, US). PANAMA. **Bocas del Toro**: 10–15 mi S from mouth of Changuinola River, *Lewis et al. 994* (GH, K, UC, US). **Chiriquí**: N of S. Felix on C. Colorado copper mine road, 5000–5500 ft, *Mori & Kallunki 5860* (MO, US). **Coclé**: El Valle, *González 32* (PMA, US). ECUADOR. **Guayas**: Riobamba, 2500 m, *Rimbach 85* (UC, US). **Pichincha**: Mt. Atacazo, 2800 m, *Mille 27* (US). **Chimborazo**: Cañon of R. Chanchan, ca. 5 km N of Huigra, 5000–6500 ft, *Camp E–3365* (US), *E–3381* (UC, US). **Azuay**: Between Cruz Pamba and Loma de Canela, region of R. Sadracay, N of Molleturo, 2315–2500 m, *Steyermark 52959* (US).

KEY TO *CAMPYLONEURUM*

1. Main lateral veins often flexuous, not or scarcely prominulous abaxially, borne at ca. a 45–60°(rarely 75°) angle to the midrib, often lacking arcuate transverse veinlets; laminae linear or rarely lanceolate or narrowly oblanceolate 29

1. Main lateral veins straight and parallel, prominulous abaxially (except in *C. occultum*), borne at ca. a 75° angle to the midrib, always bearing arcuate transverse veins with 2—several unbranched, included veinlets; laminae (or pinnae) lanceolate, oblanceolate, or broadly to narrowly lanceate 2

2(1). Laminae simple 4

2(1). Laminae pinnate 3

3(1). Pinnae 2.5–4.5 cm wide; sori 2 between the main lateral veins (Martinique, Venezuela, Colombia, Brazil) ..... *C. decurrens* (Raddi) C. Presl

3(1). Pinnae 6–10 cm wide; sori (2)3–4 between the main lateral veins (Panama to Venezuela & Bolivia) ..... *C. magnificum* T. Moore

4(2). Stipes spaced evenly along the long-creeping to very long-creeping (or rarely short-creeping) rhizomes 13

4(2). Stipes approximate, clustered near the apex of the short-creeping rhizomes 5

5(4). Laminae usually less than 6 cm wide 9

5(4). Laminae usually at least 6 cm wide (to 4 cm wide in *C. phyllitidis* from South America) 6

6(5). Venation regular, with 3 free, acroscopic included veinlets, the lateral 2 fertile, the middle one sterile and prolonged, sometimes forming a pair of areolae; sori in 2(3) regular rows between the main lateral veins (Florida, the Bahamas; Mexico to Bolivia; Venezuela to the Guianas and C Brazil) .... *C. phyllitidis* (L.) C. Presl

(6)5. Venation irregular, with varying included veinlets and areolae; sori in 2–3(4) irregular rows between the main lateral veins 7

7(6). Transverse veins not prominulous on the abaxial surface of the laminae, often hidden. Laminae subcoriaceous, firm (Greater & Lesser Antilles; Mexico to Bolivia; Venezuela to Trinidad & NW Brazil) ..... *C. latum* T. Moore

7(6). Transverse veins decidedly prominulous on the abaxial surface of the laminae 8

8(7). Laminae coriaceous, long-decurrent at the base (Ecuador to Bolivia) ..... *C. pascoense* R. Tryon & A. Tryon

8(7). Laminae membranaceous-papyraceous, short-decurrent at the base (Bolivia & Argentina) ..... *C. tucumanense* (Hieron.) Ching

9(5). Main lateral veins abaxially not prominulous, straight or not 12

9(5). Main lateral veins abaxially prominulous and straight 10

10(9). Stipes ca. 1/4 as long as the laminae; sori ca. 1 mm in diam.; rhizome scales slightly bicolorous with a yellowish central area (Costa Rica; Colombia & Ecuador) ..... *C. multipunctatum* (Christ) Lellinger

10(9). Stipes 1/3–1/2 as long as the laminae; sori ca. 2 mm in diam 11

11(10). Laminae repand, lanceate, widest at the middle (Mexico & Guatemala) ..... *C. tenuipes* Maxon

11(10). Laminae entire, narrowly lanceolate, widest below the middle (Colombia) ..... *C. nitidissimum* (Mett.) Ching

12(9). Laminae narrowly oblanceolate, attenuate at the base, usually strongly white-dotted on the adaxial surface, (5)6–10 times longer than wide; stipes 1–4(5) cm long (Mexico to Costa Rica) ..... *C. xalapense* Fée

12(9). Laminae mostly elliptic to oblong, acute or acuminate at the base, not white-dotted on the adaxial surface, (3)4–5(6) times longer than wide; stipes (2)4–14 cm long (Florida, Greater Antilles, Mexico to Colombia, Venezuela, Trinidad, the Guianas & C Brazil) ..... *C. costatum* (Kunze) C. Presl

13(4). Laminae broadly to narrowly oblaceolate (tapered more gradually toward the base than the apex) or linear (tapered about equally toward the base and apex); stipes usually less than 1/3 as long as the laminae 19

13(4). Laminae broadly to narrowly elliptic or elliptic-lanceate, tapered about equally at the base and the often caudate apex; stipes usually 1/3–2/3 as long as the laminae 14

14(13). Rhizome scales usually weakly bicolorous, pale reddish–brown in mass; laminae lanceate, mostly at least 2.5 times longer than wide 17

14(13). Rhizome scales concolorous, usually tan to golden in mass, markedly spreading (brown and readily deciduous and the rhizomes often greenish in *C. brevifolium*); laminae broadly elliptic or elliptic-lanceate, mostly 2–2.5 times longer than wide (ca. 3 times in *C. brevifolium*) 15

15(14). Laminae 2–5 cm wide, 4–14 cm long, especially the adaxial surface shiny; sori ca. 1–2 mm in diam. (Costa Rica & Panama) .. *C. sublucidum* Christ

15(14). Laminae 8–12 cm wide, 30–40 cm long, the surfaces not shiny . 16

16(15). Laminae acute at the base; sori ca. 3 mm in diam. (Colombia & Peru) ..... *C. inflatum* M. Meyer ex Lellinger

16(15). Laminae acuminate at the base; sori ca. 1–2 mm in diam. (Costa Rica to Venezuela & Bolivia) ..... *C. brevifolium* (Link) Link

17(14). Rhizome scales appressed, usually not persistent, except for some of the scale bases, not reddish in mass; rhizomes (1)1.5–3 mm in diam., greenish or turning black in age (Costa Rica & Panama; Ecuador) ..... *C. wercklei* (Christ) Lellinger

17(14). Rhizome scales spreading, persistent, often reddish in mass; rhizomes (2)3–4.5 mm in diam., not greenish 18

18(17). Rhizomes 2–4 mm in diam., stramineous; rhizome scales concolorous, pale reddish-brown in mass, strongly clathrate, slightly iridescent, the lumina translucent (Venezuela & Colombia) .... *C. sphenodes* (Kunze) Fée

18(17). Rhizomes (2)3–4.5 mm in diam., dark brown or blackish; rhizome scales weakly bicolorous, medium brown, often with paler margins, clathrate, not iridescent, the lumina yellowish (W Venezuela & Colombia) ..... *C. macrosorum* Fée

19(13). Rhizomes very long-creeping, 1.5–2.5(3) mm in diam.; laminae herbaceous, flexible 24

19(13). Rhizomes 3–9 mm in diam.; laminae papyraceous to subcoriaceous, firm 20

20(19). Laminae acute-acuminate at the base, abruptly tapered to a long, narrowly alate stipe, widest near the base. Rhizome scales acicular, blackish (Venezuela to Bolivia & Brazil) ..... *C. coarctatum* (Kunze) Fée

20(19). Laminae acuminate at the base, gradually tapered 21

21(20). Rhizome scales subappressed, suborbicular to broadly ovate, the cells mostly isodiametric. Laminae 3–7 cm wide (S Brazil, N Argentina, Uruguay, Paraguay) ..... *C. major* (Hieron. ex Hicken) Lellinger

21(20). Rhizome scales spreading, lanceolate, the central cells longer than wide 22

22(21). Stipes ca. 2 cm long; laminae narrowly elliptic-oblanceolate; rhizome scales spreading, the central cells 3–4 times longer than wide (SE Brazil) ..... *C. wacketii* Lellinger

22(21). Stipes 4–15 cm long; laminae linear (or rarely narrowly elliptic in *C. cochense*); rhizome scales lax and appressed, the central cells 1–2 times longer than wide 23

23(22). Rhizomes 5–8 mm in diam.; main lateral veins prominulous; rhizome scales dark brown in mass. Rhizome scales auriculate, with curved, overlapping auricles (W Venezuela and Colombia to Ecuador) ..... *C. cochense* (Hieron.) Ching

23(22). Rhizomes 3–4(6) mm in diam.; main lateral veins usually immersed in the lamina tissue; rhizome scales reddish-brown in mass (SE Brazil & Paraguay) ..... *C. fallax* Fée

24(19). Main lateral and transverse veins all hidden in the lamina tissue; abaxial surface of the laminae sparsely pilosulous, the hairs pale or reddish, ca. 0.25 mm long (S Mexico to Venezuela, Bolivia & Brazil) ..... *C. occultum* (Christ) L. D. Gómez

24(19). Main lateral veins and often the transverse veins prominulous; abaxial surface of the laminae glabrous 25

25(24). Apex of the rhizome scales narrow, acicular, the scales usually spreading 27

25(24). Apex of the rhizome scales, wide, obtuse to round, the scales always appressed 26

26(25). Stipes 0–3 cm long; rhizome scale cells ca. isodiametric, not contorted (Peru & Bolivia) ..... *C. ophiocaulon* (Klotzsch) Fée

26(25). Stipes 5–15 cm long; rhizome scale cells 2–3 times longer than wide, contorted (SE Brazil, Paraguay, NE Argentina) ..... *C. herbaceum* (Christ in Schwacke) Ching

27(25). Laminae (2)2.5–.35(5) cm wide, acuminate at the base; rhizome scales biauriculate, with an expanded base (Mexico to W Venezuela & Peru) ..... *C. serpentinum* (Christ) Ching

27(25), Laminae (2.5)3–8 cm wide, mostly cuneate at the base; rhizome scales peltate, little expanded at the base 28

28(27). Rhizome scales weakly bicolorous, pale brown, with broad, pale,

slightly erose-toothed margins, ca. 3 mm long, 0.75–1 mm wide (Jamaica, Puerto Rico, Lesser Antilles; S. Mexico to Bolivia; Venezuela to the Guianas & C Brazil) . . . . . *C. repens* (Aublet) C. Presl

28(27). Rhizome scales essentially concolorous, dark brown, sometimes with very narrow, paler, entire margins, ca. 4–5 mm long, 0.5–0.75 mm wide (French Guiana; Colombia to Bolivia) . . . . . *C. fuscosquamatum* Lellinger

29(1). Rhizomes (1)1.5–8 mm in diam., short- to long-creeping; laminae linear or rarely narrowly oblanceolate 33

29(1). Rhizomes ca. 1 mm in diam., very long-creeping, often with reddish, spreading scales; laminae narrowly lanceate or rarely narrowly lanceolate, acute or sometimes acuminate at the base 30

30(29). Stipes equalling the laminae (Hispaniola) . . . . . *C. oxypholis* (Maxon) Ching

30(29). Stipes 1/4–1/2 as long as the laminae 31

31(30). Rhizome scales twisted and involute, indistinctly clathrate (Hispaniola; Ecuador to Bolivia & Brazil) . . . . . *C. vulpinum* (Lindman) Ching

31(30). Rhizome scales plane, distinctly clathrate 32

32(31). Rhizome scales lanceolate from a peltate base, the cells of the base contorted; stipes 1/4–1/3(1/2) as long as the laminae (Costa Rica & Panama) . . . . . *C. falcoideum* (Kuhn ex Hieron.) M. Meyer ex Lellinger

32(31). Rhizome scales nearly linear from a narrow, peltate base, the cells of the base only slightly contorted; stipes (1/3)1/2 as long as the laminae (Venezuela to Ecuador) . . . . . *C. chrysopodum* (Klotzsch) Fée

33(29). Laminae not *Vittaria*-like, at least 1 cm wide 39

33(29). Laminae *Vittaria*-like, 0.25–0.75(1) cm wide, ca. 30 cm long . . . 34

34(33). Rhizome scales gray-brown in mass, the cell walls thin, the scales strongly clathrate, slightly iridescent (Peru to Argentina & Brazil) . . . . . *C. aglaolepis* (Alston) de la Sota

34(33). Rhizome scales pale to dark brown in mass, the cell walls thick, the scales clathrate, slightly iridescent only in *C. centrobrasilianum* 35

35(34). Rhizome scale cells contorted, slightly iridescent (C Brazil) . . . . . *C. centrobrasilianum* Lellinger

35(34). Rhizome scale cells not contorted, not iridescent 36

36(35). Rhizome scales rather broadly ovate and lax, the cells about as long as wide. Laminae commonly revolute and curled when dry or at maturity (Mexico to El Salvador) . . . . . *C. ensifolium* (Willd.) J. Smith (see note 1)

36(34). Rhizome scales more or less lanceolate, firm, and spreading, the cells at least twice as long as wide 37

37(36). Rhizome scales lanceolate from a peltate base; laminae usually strongly revolute when dry or at maturity (tropical America) . . . . . *C. angustifolium* (Swartz) Fée

37(36). Rhizome scales acicular or lanceolate from a cordate base; laminae usually plane and straight when dry or at maturity 38

38(37). Rhizome scales acicular from a dilated, cordate base with

asymmetrically overlapping auricles, ca. 3 cells wide at the midpoint (Peru & Bolivia) . . . . . *C. angustipaleatum* (Alston) M. Meyer ex Lellinger

38(37). Rhizome scales narrowly lanceolate from a cordate base with asymmetrically overlapping auricles, ca. 5 cells wide at the midpoint (Peru, Bolivia & Brazil) . . . . . *C. austrobrasilianum* (Alston) de la Sota

39(33). Rhizome scales firm, spreading, usually narrowly lanceolate; rhizomes usually pruinose **44**

39(33). Rhizome scales lax, often appressed or subappressed, ovate (except lanceolate in *C. cooperi* and *cubense*); rhizomes not pruinose (slightly so in *C. cooperi*) **40**

40(39). Laminae firm, shiny, linear **42**

40(39). Laminae flexible, dull, narrowly lanceate or oblanceolate **41**

41(40). Laminae tapered very gradually toward the base, narrowly oblanceolate, the main lateral veins slightly sinuous, at a 45–60° angle to the midrib; rhizomes 2–3 mm in diam. (Cuba, Jamaica, Hispaniola) . . . . . *C. cubense* Fée

41(40). Laminae tapered about equally toward the base and apex, narrowly lanceate; main lateral veins flexuous, at ca. a 75° angle to the midrib; rhizomes ca. 2 mm in diam. (Peru to Argentina, Paraguay & SE Brazil) . . . . . *C. lapathifolium* (Poiret) Ching

42(40). Laminae medium green, caudate at the apex; rhizomes long-creeping. Rhizomes ca. 5 mm in diam., the scales pale brown throughout (Venezuela to Bolivia) . . . . . *C. densifolium* (Hieron.) Lellinger

42(40). Laminae yellow-green, acute to acuminate at the apex; rhizomes short-creeping **43**

43(42). Laminae acuminate at the base, the stipes 2–6 cm long; rhizomes 2–4 mm in diam., the scales dark brown with paler margins (SE Brazil) . . . . . *C. rigidum* J. Smith

43(42). Laminae attenuate at the base, the stipes obsolete or nearly so; rhizomes 3–5 mm in diam., the scales medium brown (Costa Rica) . . . . . *C. cooperi* Lellinger

44(39). Rhizome scales stramineous (rarely pale brown), not clathrate, very long and narrow and filiform at the easily broken apex, the margins sparsely and irregularly serrulate-toothed (Venezuela to Bolivia) . . . . . *C. chlorolepis* Alston

44(39). Rhizome scales pale to dark brown, subclathrate or clathrate . . . **45**

45(44). Rhizome scales linear-lanceolate, 5–10 times longer than wide; rhizomes 2–3(4) mm in diam **48**

45(44). Rhizome scales lanceolate or ovate-lanceolate, 2-5 times longer than wide; rhizomes 3–5 mm in diam **46**

46(45). Rhizome scales broadly ovate, ca. 2 times longer than wide; laminae usually not revolute, the midribs sparsely scaly (Bolivia & Argentina) . . . . . *C. lorentzii* (Hieron.) Ching

46(45). Rhizome scales lanceolate, 3–5 times longer than wide; laminae often revolute, the midribs usually not scaly **47**

47(46). Central cells of the rhizome scales nearly straight, occasionally

contorted (the scales typically 5–7 mm long, 1.5–2 mm wide, concolorous); lateral veins prominulous (Cuba, Jamaica, Hispaniola; Mexico to Venezuela & Bolivia) . . . . . *C. amphostenon* (Kunze ex Klotzsch) Fée

47(46). Central cells of the rhizome scales strongly contorted; lateral veins immersed in the lamina tissue, usually obscure (Costa Rica to Bolivia) . . . . . *C. irregulare* Lellinger

48(45). Rhizome scales peltate, lacking auricles 50

48(45). Rhizome scales auriculate, the auricles often overlapping and the scales appearing to be peltate 49

49(48). Rhizome scales lanceolate with an expanded base, brown or pale brown, the basal auricles decidedly overlapping, the scales often appearing peltate (Colombia to Bolivia) . . . . . *C. solutum* (Klotzsch) Fée

49(48). Rhizome scales linear to narrowly lanceolate, dark reddish-brown, the basal auricles not or only slightly overlapping (Peru & Bolivia) . . . . . *C. asplundii* (C. Chr. in Aspl.) Ching (see note 2)

50(48). Stipes mostly 1–3 cm long, ca. 0.25 cm distant; rhizome scales brown in mass, typically 3–4 mm long, 0.5–0.75 mm wide, usually bicolorous, the margins pale (Florida; Greater Antilles; Guadeloupe; Mexico to Bolivia & Brazil) . . . . . *C. angustifolium* (Swartz) Fée

50(48). Stipes mostly 8–25 cm long, 1–1.5 cm distant; rhizome scales dark reddish-brown in mass. Rhizome scale attachment point very large (W Venezuela & Colombia to Peru) . . . . . *C. remotifolium* (Hieron.) Lellinger

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Note 1. This name is based on a specimen ostensibly from Peru, collected by Nee (B-Hb. Willd. 19610). All the specimens I have seen of this species are from Mexico to El Salvador, none have been from South America. It is known that the Malespina Expedition stopped in Guatemala and at Acapulco, from where Nee journeyed to the Mexican capital. Thus it is possible that the collection is mislabelled.

Note 2. The earlier name *C. leucorhizon* (Klotzsch) Fée may apply to this species if it is lectotypified on the one Peruvian syntype. But the name is based on mostly Venezuelan syntypes, and if it is lectotypified on a Venezuelan syntype, the name probably does not apply to this central Andean species. The name *C. asplundii*, although later, can be applied without doubt to this species.

Literature Cited

Tryon, R. M. and A. F. Tryon. 1982. *Ferns and allied plants, with special reference to tropical America*. New York: Springer-Verlag.

Wagner, W. H., Jr. and D. R. Farrar. 1976. The Central American fern genus *Hyalotricha* and its family relationships. Syst. Bot. 1:348–362.

American Fern Journal 78(1): 35–36 (1988)

Isoëtes pallida, a New Species from Mexico

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During preparation of the *Isoëtes* treatment for the Flora Mesoamerica it has become evident that a collection of *Isoëtes*, from Oaxaca, Mexico, formerly recognized as a disjunct population of the Venezuelan *I. triangula* (Hickey, 1985) represents a new species.

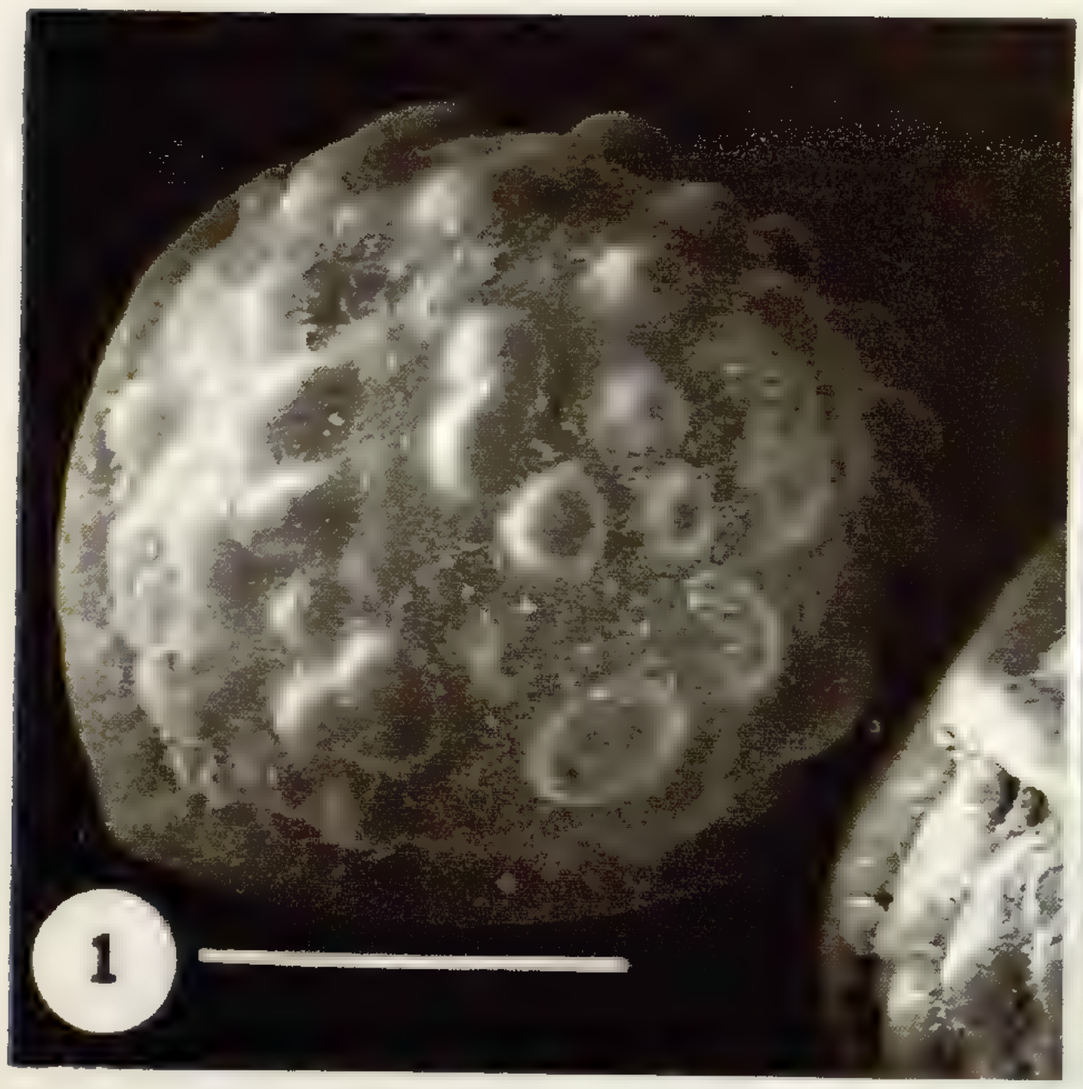
Isoëtes pallida Hickey, sp. nov.—Type: Mexico, State of Oaxaca, 4 mi W of Costa Rica, rain ponds along Hwy 190, sandy soil with scattered boulders, 3 Aug 1965, *Kral 25320* (holotype MO!; isotypes MICH! VDB!).

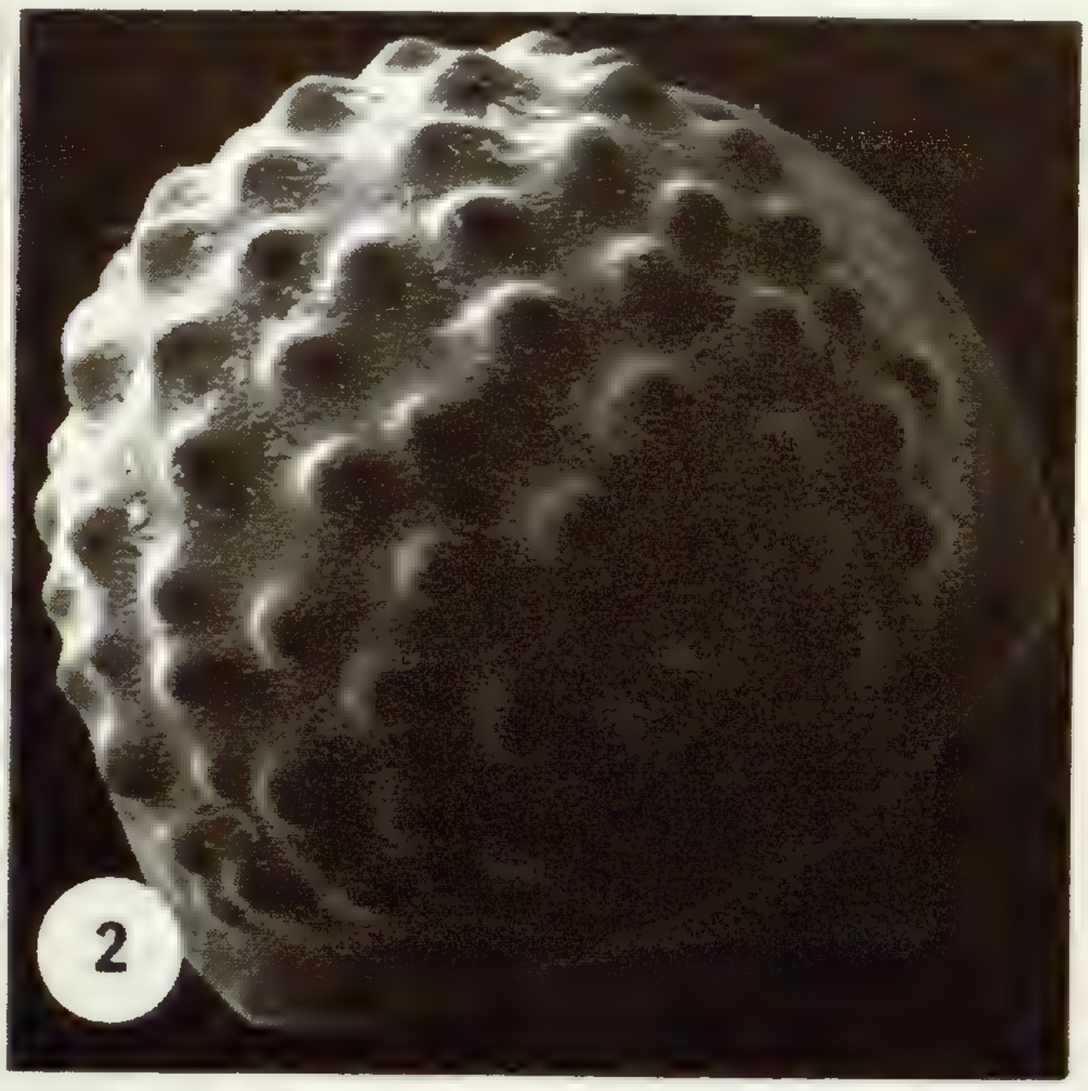
A *I. triangula* sporangiis non-pigmentiferis et macrosporis minoribus, a *I. cubana* pustulis megasporarum acutis, numerosioribus differt.

Corm globose, two- or three-lobed; roots dichotomous. Leaves 20–45, to 300 mm long, 4.5–8.0 mm wide at the base, 0.5–1.5 mm wide at mid-length, stiffly erect; alae 30–80 mm long [15–22 (37)% of the total leaf length], 1–1.5 mm wide at the sporangium, chartaceous and nearly transparent, each apex attenuate; subula trigonal, stramineous to bright green, the apex attenuate; peripheral fibrous bundles distinct; stomates present; scale leaves present, phyllopodia absent. Sporangia 3.6–4.0 mm long, 2.5–4.0 mm wide, ovate, tan, unspotted, basal. Vela absent. Ligules not seen. Labia 0.9–1.5 mm high, 1.0–1.2 mm wide, depressed-ovate to widely depressed-ovate, submembranaceous, tan, erose-entire to mucronate, the mucro to 0.45 mm long. Megaspores 390–460 ($\bar{x}=426$) μm diam., white, pustulate, with 70 or more pustules on the distal surface, these subacute and evenly distributed and equally well developed on all surfaces, rarely anastomosing; equatorial and proximal ridges distinct, triangular in cross-section, the equatorial ridges rarely scalloped; microspores not seen. $2n=44$.

Paratype: Mexico. Oaxaca, Mpio. Miltepec, 11.8 mi NW of Zanatepec along Hwy 190, dominant plant in shallow rain pools in open 'savanna' vegetation, soil a thick gray clay, 19 Oct 1986, *Hickey & Russell 962* (GH, MU, NY).

Isoëtes pallida resembles members of the *I. triangula* species complex of central Venezuela, northern Brazil, and Guyana, but differs in having an unpigmented sporangium and somewhat smaller megaspores (perhaps a reflection of ploidy differences). It is also extremely close, morphologically, to *I. cubana* of Cuba, Belize, and the Yucatan peninsula, Mexico. It differs from that species in chromosome number (*I. cubana* is a diploid with $2n=22$), the number of pustules per megaspore, and slight differences in the shape of the pustules, which are more rounded in *I. cubana* (Figs. 1 and 2). Preliminary allozyme data (Hickey, unpublished) support a close evolutionary relationship between *I. cubana* and *I. pallida*. Both of these species belong to a larger complex, the *I. panamensis* alliance, which is characterized by distinctly trigonal (sharply 3-angled) subulae and prominent scales or phyllopodia. The *panamensis* alliance is a large, and as yet poorly understood group found from Paraguay to





FIGS. 1 AND 2. Scanning electron micrographs of *Isoëtes* megaspore surface morphology. FIG. 1. *I. cubana, Wright s.n.* (MO). FIG. 2. *I. pallida, Kral 25320* (MICH). Bar = 200 μm.

southeastern and western North America. The group includes several widely dispersed and well known species such as *I. butleri, I. nuttallii, I. orcuttii, I. melanopoda, I. flaccida, I. howellii,* and *I. mexicana.*

Isoëtes pallida grows in exposed, low scrub habitat of southwestern Mexico very close to the Oaxaca-Chiapas border. To date, only two collections have been made, both probably from the same locality. The paratype material was collected from a small ephemeral rain pool approximately 30 feet in circumference. The maximum water depth of the pool at the time of collection was 12 inches but had obviously dropped considerably in the previous weeks. Plants were found in equal abundance on the muddy shore and in the deepest parts of the pool. It seems likely that at least some of the plants were completely submerged before the water level dropped.

This species, like many other tropical *Isoëtes*, is strongly seasonal. The Kral collection, made in August, contains numerous, well-developed, intact megasporangia. The October collection of Hickey and Russell contains only sporangial remnants and scattered megaspores indicating that the aesitvation process had commenced. In addition, when split lengthwise, specimens of the October collection showed that the apical meristem had already begun initiating a series of scales. Such scales are hypothesized to function as protective organs for the meristem during periods of drought and aestivation (Hickey, 1986a).

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LITERATURE CITED

HICKEY, R. J. 1985. Revisionary studies of neotropical *Isoëtes*. Ph.D. dissertation. The University of Connecticut, Storrs.

———. 1986a. The early evolutionary and morphological diversity of *Isoëtes*, with descriptions of two new neotropical species. Syst. Bot. 11:309–321.

———. 1986b. *Isoëtes* megaspore surface morphology: nomenclature, variation, and systematic importance. Amer. Fern J. 76:1–16.

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Periodic Censuses (1916–1986) of *Phyllitis scolopendrium* var. *americana* in Central New York State

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This report presents seventy years of census data for the central New York populations of *Phyllitis scolopendrium* (L.) Newman var. *americana* Fern., the American hart's-tongue. *Phyllitis scolopendrium* was first discovered in North America near Syracuse, New York, in 1807 (Maxon, 1900). Currently, populations occur in two rather distinct areas: along the Niagara Escarpment in Ontario (Soper, 1954), on the Upper Peninsula of Michigan (Futyma, 1980), and in central New York (Faust, 1969); and in sinkholes in eastern Tennessee (McGilliard, 1936) and northern Alabama (Short, 1979). *Phyllitis scolopendrium* is listed as endangered in each state where it occurs; it is currently under review for listing as threatened or endangered in the United States by the U.S. Fish and Wildlife Service.

The largest number of *P. scolopendrium* individuals in the United States occurs in the combined populations within central New York, in Onondaga and Madison counties. There are currently about 15 locations for *P. scolopendrium* in New York (Faust, 1960). Six locations, or substations, occur at Clark Reservation State Park in Jamesville, New York. The substations at Clark Reservation are particularly important because most of the *P. scolopendrium* in New York exist here; in 1966, approximately 96% of all mature *P. scolopendrium* in New York (1228 total) occurred here (Faust, 1969).

The substations at Clark Reservation are also unique in that a census of the population at each substation was begun in 1916 by M. Hunter (1922). Populations at each substation were censused again in 1920 by Hunter. The next census was done in 1936 by M. Faust with assistance from the Syracuse Botanical Club and botany graduate students at Syracuse University. Since 1936, the population at each substation at Clark Reservation has been inventoried about every five years. The last census that was reported in the scientific literature was made in 1956 (Faust, 1960). The objective of this paper is to report results of inventories made about every five years since 1956, including the most recent census, undertaken by the first author in 1986. Seventy years of monitoring data are also examined in relation to potential habitat requirements and conservation measures.

STUDY AREA

Clark Reservation State Park is located in north-central Onondaga county, about 8 km southeast of Syracuse. In 1915, Mary Clark Thompson gave to the state of New York 43.7 ha as a memorial for her father, Myron H. Clark, who was

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governor of New York in 1855. In 1926, Clark Reservation was established as a state park and was acquired by the New York State Museum as part of a preservation program for notable geologic features. Today, the park covers about 121.4 ha over a landscape that varies from gently rolling, to extremely steep grades in the plunge basins and glacial channels. Elevations range from 174 to 235 m. There are over 400 species of vascular plants within the park, including about 30 fern species (Egler, 1943; Faust, unpublished).

Descriptions of Substations

The physical characteristics of each substation are probably the dominant influence on the extent, size, and vigor of each *P. scolopendrium* population. Therefore, a brief description of each substation follows. This species is generally restricted to northeast-facing slopes on talus. Locations of particular substations at Clark Reservation can be furnished upon a request to the authors.

Substation I is enclosed on three sides by ravine walls; there is no wall to the east. Because of this opening, the ravine is less protected from the wind and slopes tend to be dry. The slope varies from 65 to 70% where *P. scolopendrium* is found; the aspect ranges from N 28° W to S 71° E. Mature, vigorous plants are often in small clumps beneath canopy openings. Loose talus covers the slopes, making this site susceptible to rockslide damage.

Substation II is enclosed on all sides by ravine walls, the east and west walls are lower in height than the north and south, and the south wall is much higher than the north. The south and west slopes remain moist throughout the year. *P. scolopendrium* is found on aspects ranging from N 06° W to S 77° E and slopes from 55 to 74%; approximately 10 mature and immature plants are found on a S 10° E aspect and 71% slope. Most *P. scolopendrium* are found at midslope; the upper slope consists of a rock outcrop and the lower slope is overgrown with *Tsuga canadensis* and *Taxus canadensis*.

Substation III, the largest area occupied by *P. scolopendrium* in Clark Reservation, also has the largest population in New York. It is enclosed entirely by ravine walls; the southwest-facing wall, in contrast to many of the other ravines, is lower in height than the northeast-facing slope on which *P. scolopendrium* occurs. This latter slope remains moist throughout the year. Individuals are both clumped under small canopy openings, or scattered throughout the ravine beneath the closed canopy. The slope ranges from 45 to 68%, and aspects from N 24° E to S 83° E, where *P. scolopendrium* is located on mid to lower slope positions. Where *Taxus canadensis* is located on the lower slope, *P. scolopendrium* is found at midslope only; the upper slope is mostly rock outcrops.

Substation IV is a relatively dry ravine, and is formed by north- and south-facing slopes. There is no barrier to the winds from the east and west, which tends to dry the slopes. *Phyllitis scolopendrium* is found at midslope positions at aspects that vary from N 07° W to N 17° W, and slopes from 52 to 72%. The upper slope consists of a rock outcrop; the lower slope is covered by *Taxus canadensis*.

Substation V supports the most vigorous individuals of *P. scolopendrium* in Clark Reservation, and also the largest number of ferns per unit area. This population is located within a glacial plunge basin. Slopes supporting the fern vary from 59 to 64%, and aspects from N 61° E to S 86° E. *Phyllitis scolopendrium* is found at midslope, in one very large patch, under a canopy opening. Various herbaceous species form a subcanopy over 1.0 m high above the ferns in the summer; this feature is not as pronounced in other substations in Clark Reservation. High humidity is maintained throughout the year in this ravine; the basin floor soils usually remain moist.

Substation VI has contained the smallest number of *P. scolopendrium* in Clark Reservation since censusing began. This is the driest substation, mainly because it faces Little Green Lake and not another ravine wall as do the other substations. This feature leaves the site very exposed to wind and subsequent drying. The fronds of *P. scolopendrium* at this substation are usually small and not lustrous, compared to the more vigorous individuals at other substations. The ferns occur at midslope, over an area of about 8 m^2, making this the smallest substation of those in Clark Reservation. The slope is 66% and has an aspect of N 50° E. The ferns are found almost exclusively in the deep crevices between boulders, or small cave-like pockets within the slope, both of which allow protection from the wind, and maintenance of constant high humidity.

Methods

The 1986 census of *P. scolopendrium* populations in Clark Reservation State Park was done according to the sweep method used in previous studies (Faust, 1960). Under this method, volunteers begin at the bottom of a slope on which the ferns are growing and slowly walk up the slope, counting individual ferns as they are seen. The sweep is initiated at the bottom of the slope since *P. scolopendrium* plants are sometimes hidden in crevices on the lower sides of rocks. Censusing requires careful coordination among volunteers so that no ferns are overlooked, or counted more than once. Because *P. scolopendrium* is evergreen, spring and fall censusing is ideal as herbaceous species do not cover the individual ferns during these periods. Leaf litter is generally moved aside during the sweep to reveal any covered ferns.

Each fern encountered during the sweep is placed in one of three categories: (1) mature (fronds usually more than 15.0 cm long; mature sporangia present on the adaxial surface of the fronds); (2) immature (fronds usually between 2.5 and 15.0 cm; sporangia absent); or (3) sporelings (fronds less than 2.5 cm long).

Results

Census data (Fig. 1) document an increase in mature and immature individuals at all sites, since 1966. However, prior to 1966, there was a decrease in the mature and immature *P. scolopendrium*. The three least protected (i.e., to wind dessication and abrupt climatic events or extremes) substations, I, IV, and VI, all show large decreases in their populations during the mid-1950s and

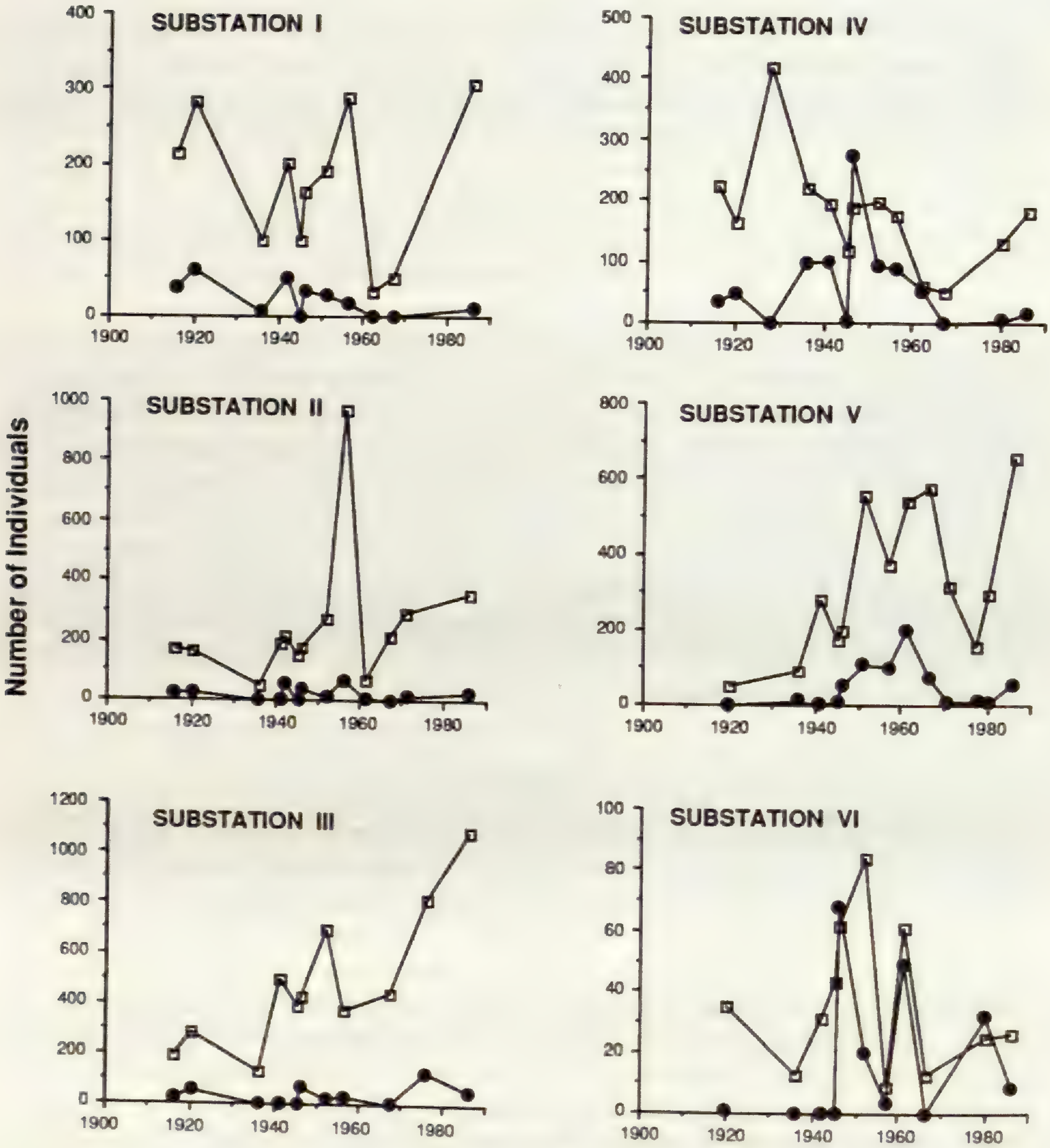

FIG. 1. Census data (1916–1986) for mature and immature (□) *Phyllitis scolopendrium* var. *americana* and sporelings (●) in central New York. Note the variations in scale for number of individuals.

mid-1960s; the moister substations, III and V, show smaller decreases during these years. Substation II, which is also moist, decreased greatly in population size during this period.

Between 1956 and 1962, the number of mature and immature ferns at substation I dropped 89% from 287 to 32; from 1967 to 1986, the population increased 502% from 51 to 307 mature and immature individuals (Fig. 1). The population at substation II had a 255% increase from 1952 (272 mature and

immature plants) to 1956 (965), and then a 93% decrease by 1961 (68). Between 1967 and 1986, this population increased 67%, from 215 to 358 mature and immature plants. Substation IV had 175 mature and immature ferns in 1956; in the following census, 1962, the population had decreased 65% to 61 mature and immature. In 1967, 51 plants were reported. A 259% increase in this population from the 1967 data occurred by the 1986 census. The population at substation VI decreased by 89% from 1952 (84 mature and immature fern) to 1957 (9). By 1961, this population had increased 578% to 61 mature and immature fern. By 1966, only 13 individuals, a 79% decrease, were found; in 1986, 26 were reported.

Substations III and V, the most mesic ones, had smaller population decreases during the mid-1950s and 1960s. Substation III data show a 47% decrease beginning with the 1952 census (699 mature and immature fern) and continuing to the 1956 census (372). This population increased 19% from 1956 to 1967 (444 mature and immature fern), and 84% from 1967 to 1976 (818); as of 1986, 1089 mature and immature ferns (a 33% increase over 1976 data) were reported. Substation V, which contains the most vigorous ferns and the greatest density, had a 33% decrease in population size between 1951 (553 mature and immature plants) and 1957 (370), and a 46% increase between 1957 and 1961 (540). A 51% decrease occurred from 316 mature and immature plants in 1971, to 156 in 1977. By 1986, the population size had increased 322% from the 1977 data.

Sporeling counts vary considerably from census to census, and may not indicate accurate trends. However, sporeling counts are often positively correlated to mature and immature fern counts at the same substation.

Discussion

Sporeling counts, although somewhat useful in indicating favorable conditions for germination, are not included in the discussion of site totals because of the potentially high error involved in censusing this size-class; they are easily missed by those doing the censusing.

Variations in census figures are most likely attributable to historical/climatic events in a given year. For example, a possible cause of the 89% reduction in population size of substation I during the mid-1950s and mid-1960s is the drought that occurred in central New York and the northeast U.S. during this period (Namias, 1966). Since substation I is one of the drier ravines, any dry period would be expected to affect the area. Populations in all other ravines also decreased during this period. The drier substations (I, IV, and VI) had larger percent decreases than the moister substations (III and V). Substation II, although moist, had a large percent decrease at this time.

Substations I, IV, and VI, which are more exposed to wind than substations II, III and V, contain the smaller *P. scolopendrium* populations. The individuals at these former locations tend to have smaller and fewer fronds than those at the moist substations, and often are found in rock crevices, where the loss of moisture to wind is lessened. Substation VI, for example, the driest of those in Clark Reservation, has the least vigorous and fewest number of *P. scolopendrium*; almost all are found in rock crevices. The population size

remains small here, existing only under a canopy opening which lets in light and precipitation, enabling growth. Adjacent forested areas do not support growth of this fern.

Growth of *P. scolopendrium* in the moister substations, II, III, and V, does not seem to be as limited as in the drier sustations. Substation V, for example, contains the most vigorous individuals in Clark Reservation. Site characteristics of this basin that maintain constant humidity are protection from the wind by ravine walls, an herbaceous subcanopy that maintains moisture at ground level, and a basin floor which remains moist throughout the year. This population showed the smallest decrease (33%) in the number of mature and immature ferns during the mid-1950s. From 1957 to 1966, the population increased 56%, while most other substations decreased.

Conifer cover seems to affect the growth of *P. scolopendrium*; the fern is rarely found beneath conifers. The effect that *Tsuga canadensis* has on soil and vegetation has been well-documented (Daubenmire, 1931; Lewin, 1975; Rogers, 1978). Whether *T. canadensis* has much of an effect on lowering soil pH which leads to cation depletion on soils derived from limestone bedrock is not known. The dense canopy of *T. canadensis* greatly reduces the limited light on the north-facing slopes to which the fern is restricted. The amount of snow that accumulates under conifer canopies as compared to adjacent hardwood areas may also be an important factor. The soils exposed under those conifers tend to freeze during the winter months; adjacent soils, under hardwood canopies, insulated by deep snow cover, do not freeze. The ability of *P. scolopendrium* to obtain moisture from the soil during the winter may be affected by the amount of snow insulation.

In 1925, about 400 mature *P. scolopendrium* were transplanted to Substation IV from a nearby site that was soon to be quarried for limestone. Although these transplants initially flourished (Faust, unpublished field notes), many did not survive beyond the early 1930's. If recovery plans are eventually developed for this species, this experience suggests that site conditions for this fern are very specific. We are currently trying to assess habitat variables to which this species is especially sensitive.

In summary, groupings of *P. scolopendrium* are found under canopy openings where more sunlight and precipitation reach the ground. In adjacent canopied areas, ferns are scattered. Rock crevices and small cave-like openings within the slope help to maintain a constant humidity near ground level. Humidity is maintained over entire slopes by the arrangement of ravine walls, which prevents drying by the wind. The largest Clark Reservation populations are found in humid, well-enclosed ravines. Fluctuations in population numbers in these areas due to extreme environmental conditions, such as drought, are smaller than in less humid ravines. Populations at all substations have increased in recent years, probably due to a lack of extreme climatic conditions.

After further habitat study is completed here, conservation measures may be suggested to maintain *P. scolopendrium* populations at current levels or possibly even increase population size. One method might be to prevent an increase in conifer cover by the removal of conifer saplings. This may likewise

be done with hardwood saplings, to maintain canopy openings. By developing propagation techniques, population numbers may be increased. Unwanted visitation to the Clark Reservation populations does not seem to be a problem for the survival of *P. scolopendrium* since the ravines in which it is found are difficult to access.

Acknowledgments

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Literature Cited

Daubenmire, R. F. 1931. Factors favoring the persistence of eastern hemlock in Indiana. Butler Univ. Bot. Stud. 2:29–32.

Egler, F. E. 1943. *The ferns and flowering plants of the Clark Reservation, Onondaga County, New York.* New York State College of Forestry Tech. Publ. No. 61, N.Y.S. College of Forestry, Syracuse, N.Y., 64 p.

Faust, M. E. 1960. Survival of Hart's-tongue fern in Central New York. Amer. Fern J. 50:55–62.

———. 1969. Conservation of the Hart's-tongue fern in North America. Biol. Cons. 1:256–257.

Futyma, R. P. 1980. The distribution and ecology of *Phyllitis scolopendrium* in Michigan. Amer. Fern J. 70:81–87.

Hunter, M. 1922. The present status of *Scolopendrium* in New York State. Amer. J. Bot. 9:28–36.

Lewin, D. C. 1975. The vegetation of the ravines of the southern Finger Lakes, New York region. Amer. Midl. Naturalist 91:315–342.

Maxon, W. R. 1900. On the occurrence of the Hart's-tongue in America. Pp. 30–46 in *Fernwort Papers*, ed. M. Slosson. Binghamton, New York: Willard N. Clute & Co.

McGilliard, E. 1936. The Hart's-tongue in Tennessee 1878–1935. Amer. Fern J. 26:113–122.

Namias, J. 1966. Nature and possible causes of the Northeastern United States drought during 1962–1965. Monthly Weather Rev. 94:543–554.

Rogers, R. S. 1978. Forests dominated by hemlock (*Tsuga canadensis*): distribution as related to site and past settlement history. Canad. J. Bot. 56:843–854.

Short, J. W. 1979. *Phyllitis scolopendrium* newly discovered in Alabama. Amer. Fern J. 69:47–48.

Soper, J. H. 1954. The Hart's-tongue fern in Ontario. Amer. Fern J. 44:129–147.

American Fern Journal 78(2): 44–67 (1988)

The *Pellaea glabella* Complex: Electrophoretic Evidence for the Derivations of the Agamosporous Taxa and a Revised Taxonomy

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Pellaea glabella Mett. ex Kuhn is a species of small ferns usually occurring in crevices of limestone rocks and cliffs across the United States and southern Canada. This species has been considered a complex of three varieties (Tryon, 1957; Tryon & Britton, 1958), one reproducing sexually and the other two agamosporously (i.e., sporophytes produce unreduced spores and gametophytes initiate new sporophytes without fertilization). *Pellaea glabella* var. *occidentalis* (E. E. Nelson) Butters comprises sexual diploid plants from the west central United States and Canada (Fig. 1, OCC). Variety *simplex* Butters consists of agamosporous tetraploids in the western U.S. and Canada (Fig. 1, SIM). Variety *glabella* consists of an agamosporous tetraploid race in the eastern and east central United States and adjacent Canada (Fig. 1, GLAa) and a more recently discovered sexual diploid race (Wagner et al., 1965) known only from Missouri (Fig. 1, GLAs). *Pellaea atropurpurea* (L.) Link is a broadly distributed agamosporous triploid species that has been proposed as one progenitor of the agamosporous taxa of *P. glabella*. Its distribution overlaps much of the range of the *P. glabella* complex, stretching from northern Guatemala, through Mexico, the west-central to eastern United States, and southeastern Canada, with disjunct stations in southern Alberta and British Columbia and in northern Saskatchewan (Tryon, 1957, 1972; Rigby, 1968).

Several hypotheses have sought to explain the evolutionary origins of the tetraploid agamosporous varieties of *P. glabella*. Tryon (1957) proposed that they arose as allopolyploids resulting from fertilization of a haploid egg of sexual *P. glabella* var. *occidentalis* by the triploid sperm of agamosporous *P. atropurpurea* [agamosporous taxa can act as male parents in crosses with archegoniate gametophytes of sexual taxa, and in such cases agamospory is always inherited (Walker, 1962)]. She hypothesized that one such hybridization could have given rise to var. *glabella* in the east and another to var. *simplex* in the west. Lellinger (1985) accepted this hypothesis for the origin of var. *simplex* (which he recognized as an independent species, *P. suksdorfiana* Butters). Alternatively, Tryon hypothesized (1957, p. 140) that they arose as autopolyploids (not involving interspecific hybridization) from sexual diploid var. *occidentalis*. Several years later, Wagner et al. (1965) discovered a sexual diploid race of *Pellaea glabella* var. *glabella* in Missouri and found it indistinguishable from agamosporous tetraploid var. *glabella* except in its chromosome number and number of spores per sporangium. They concluded that this new sexual race made unlikely the origin of agamosporous var. *glabella*

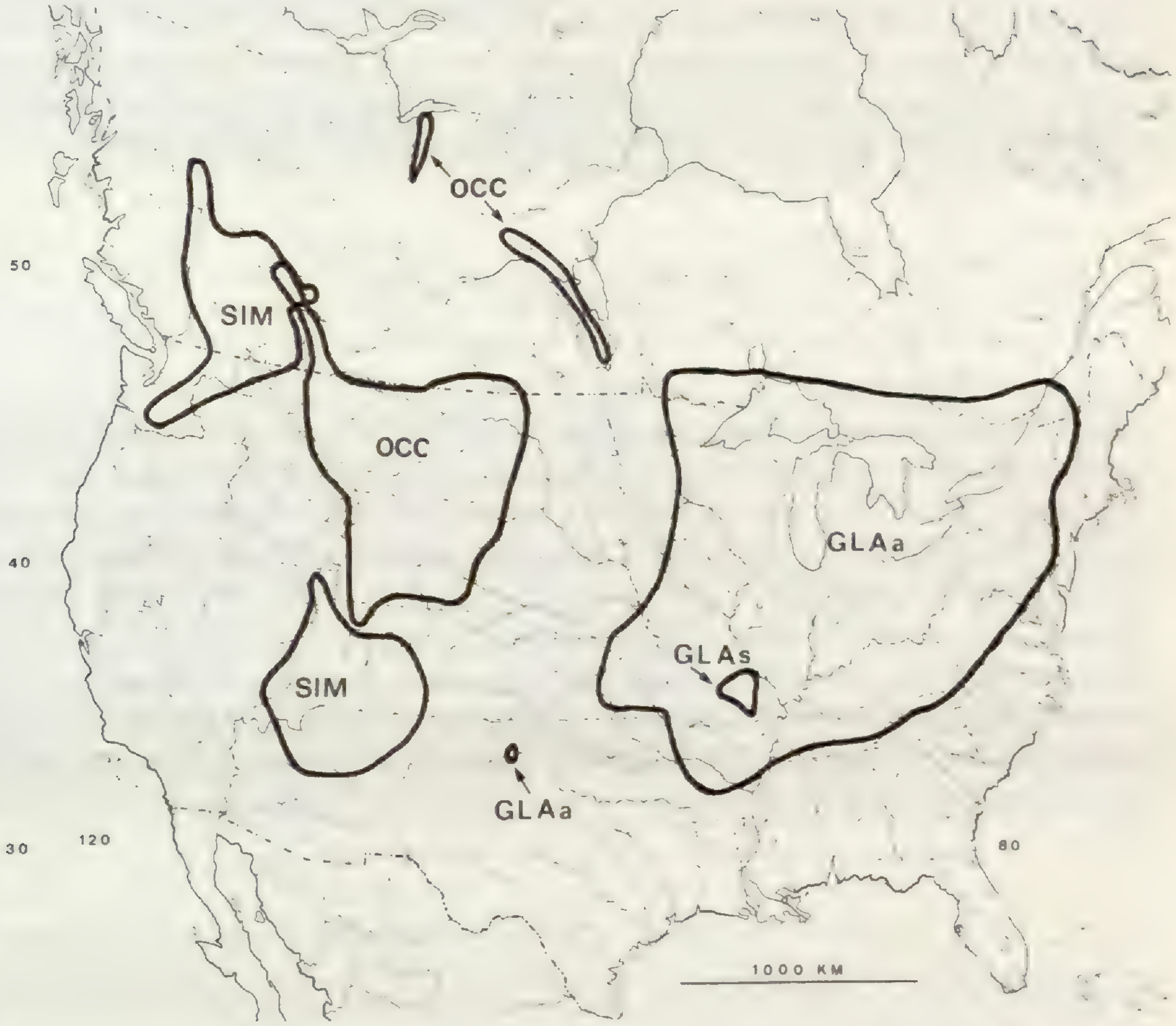

FIG. 1. Geographic ranges of the four taxa in the *Pellaea glabella* complex. SIM = *P. glabella* var. *simplex*, OCC = *P. glabella* var. *occidentalis*, GLAa = agamosporous race of *P. glabella* var. *glabella*, GLAs = sexual race of *P. glabella* var. *glabella*.

as a hybrid between *P. atropurpurea* and *P. glabella* var. *occidentalis*. Instead, they suggested that the agamosporous tetraploid was more likely an autotetraploid derivative of the sexual diploid of the same variety. The latter view was accepted by Lellinger (1985). Several other hypotheses are made possible by the presence of two sexual taxa in this complex. *Pellaea atropurpurea* might have sired the agamosporous races through hybridization with the respective sexual entities, or the sexual entities might have initiated respective agamosporous varieties via autopolyploidy, or the agamosporous varieties might have arisen via crosses between variant genotypes of the two sexual entities. Rigby and Britton (1970) stressed the need for a more thorough biosystematic study of these taxa in order to clarify the evolutionary relationships among them.

Enzyme electrophoresis is a valuable technique for elucidating the derivations of polyploids because genes coding isozymes in progenitor taxa are additive in offspring resulting from crosses and because alleles coding allozymes are expressed co-dominantly (Roose & Gottlieb, 1976; Gottlieb, 1982; Haufler et al., 1985; Werth et al., 1985; Gastony, 1986). Enzyme variants coded by the genes of

progenitor taxa can therefore be used as markers to trace the ancestry of phyletic derivatives. This paper uses taxon-specific banding patterns of six polymorphic enzymes to test both the hypothesized role of *P. atropurpurea* in the origin of the agamosporous varieties of *P. glabella* and the origins of those varieties from the respective sexual taxa of this complex.

Materials and Methods

The taxonomy and nomenclature of Tryon (1957) are provisionally followed throughout this paper up to the final section entitled Taxonomic Conclusions, where they are revised to reflect insights gained in this study. Following Walker (1979), the term "agamosporous" (Löve & Löve, 1975) is used here in place of "apogamous" or "apomictic" for fern taxa in which the production of unreduced spores and apogamous sporophyte initiation occur regularly in the life cycle. The geographic ranges of *P. glabella* (Fig. 1) and *P. atropurpurea* are based on Tryon (1957, 1972), Tryon and Britton (1958), Wagner et al. (1965), Rigby (1968), Rigby and Britton (1970), Brunton and Lafontaine (1974), and Brunton (1979). Live population samples of the sexual and agamosporous varieties of *P. glabella* were collected from throughout their ranges, and *P. atropurpurea* was sampled over a large part of its distribution (Table 1). Voucher specimens are deposited at IND.

Table 1. Locality Data for Cited Populations of *Pellaea* Species Examined Electrophoretically.

P. glabella var. *simplex*. **S1**—British Columbia, Pavillion Lake, ca. 24 mi NW of Cache Creek, limestone outcrops along Rte. 12, *Gastony 82–17*; **S2**—Washington, Douglas Co., ca. 7 mi NE of Palisades, Rainy Cave, Rooster Rock Ranch, *Gastony 82–19*; **S3**—Washington, Grant Co., Crescent Bar, ca. 10 mi from Quincy, in shallow caves of basaltic SW-facing cliffs across from Crescent Bar condominiums, *Gastony 82–20*; **S4**—Colorado, Garfield Co., ca. 14 mi NE of Rifle, limestone cliffs 1 mi beyond fish hatchery, *Gastony 82–23*; **S5**—Arizona, Coconino Co., Flagstaff, limestone outcrops along Rio de Flag, *Gastony 82–25*; **S6**—British Columbia, limestone outcrops along road from Williams Lake to Riske Creek, E side of Fraser River, *Gastony 82–18*.

P. atropurpurea. **A1**—Arizona, Cochise Co., Huachuca Mts., Fort Huachuca Military Installation, near mouth of Scheelite Canyon, *Yatskievych 82–271*; **A2**—Arkansas, Benton Co., S. of Bella Vista and NE of Rte. 71, along old country road, *Yatskievych & McCrary 83–60*. **A3**—Missouri, Pulaski Co., Gasconade River at Rte. 7, between Richland and Lequey, on boulders beside dirt road along river, *Gastony 82–27A*; **A4**—Missouri, Jefferson Co., 2 mi E. of Antonio on Highway M, disturbed wooded hillside with limestone outcrops, *Gastony 83–33*; **A5**—West Virginia, Pendleton Co., limestone outcrops, Smoke Hole recreational area, *Gastony 83–48*; **A6**—West Virginia, Jefferson Co., Shepherdstown, cliffs along River Road, *Gastony 83–49*; **A7**—Virginia, Giles Co., limestone cliffs near New River Cave at Goodwin's Ferry, *Werth s.n.* = *Gastony 82–30*; **A8**—Pennsylvania, Centre Co., ca. 3 mi NE of State College, NW-facing limestone cliffs at Big Rock along Spring Creek, *Gastony 82–28*; **A9**—New Jersey, Sussex Co., Andover, limestone outcrops along abandoned RR line N of Rte. 206, *Gastony 83–53*; **A10**—Maryland, Washington Co., cliffs upstream from Dam 5 on Potomac River, *Gastony 83–51*; **A11**—Vermont, Chittenden Co., E of Burlington, limestone along RR cut between Rte. 15 and Winooskie River gorge, *Gastony 83–54A*; **A12**—Quebec, Gatineau Co., 3 mi S of Poltimore, SW-facing cliff on Chamberlin property, *Gastony 83–58*; **A13**—Arkansas, Benton Co., Bella Vista, trout farm catfish pool #3, on S- and W-facing limestone cliffs near grotto E of pool, *Yatskievych & McCrary 83–61*; **A14**—Maryland, Washington Co., along the Potomac River at the Rte. 34 bridge SW of Sharpsburg, *Gastony 83–50*; **A15**—Missouri, Jefferson Co., river bluffs 10 miles W of DeSoto, near junction of road H and Big River, *Gastony 83–34*; **A16**—Texas, Davis Co.,

TABLE 1. *continued*

Madera Canyon, hillside above rest area on Rte. 118, *Gastony 87–8*; **A17**—Nuevo Leon, México, Cañon de San Francisco, W of Rte. 85, ca. 35 km SE of Monterrey, dry streambed across road from pumping station, *Gastony 87–11–7*.

P. glabella var. *glabella*, agamosporous tetraploid. **G1**—Ontario, Guelph, limestone walls of old quarry on reformatory property, *Gastony 83–60*; **G2**—Minnesota, Winona Co., Whitewater State Park, limestone outcrops near Chimney Rock and Inspiration Point, *Gastony 82–1*; **G3**—Missouri, Dent Co., Montauk State Park, limestone bluffs along creek near picnic grounds, *Werth s.n.* = *Gastony 82–43*; **G4**—New Jersey, Hunterdon Co., Bloomsbury, on mortar between stones of RR bridge, *Gastony 83–52*; **G5**—Vermont, Chittendon Co., Ethan Allen Park N of Burlington, limestone outcrops, *Gastony 83–55*; **G6**—Quebec, Papineau Co., 2 mi SW of Poltimore, SW-facing cliff, *Gastony 83–57*; **G7**—Texas, Potter Co., limestone outcrops near Rte. 287 crossing of John Rey Creek, *Gastony 82–26*; **G8**—Pennsylvania, Centre Co., ca. 3 mi NE of State College, NW-facing limestone cliffs of Big Rock along Spring Creek, *Gastony 82–28*; **G9**—Virginia, Giles Co., limestone cliffs near New River at Goodwin's Ferry, *Werth s.n.* = *Gastony 82–29*; **G10**—Missouri, Jefferson Co., bluffs along Big River on road Y, across road from Bethlehem Church, ca. 4 mi SE of Grubville, *Gastony 83–35*; **G11**—Missouri, Shannon Co., limestone outcrops SW of bridge at Rte. 19 crossing of Current River, *Gastony 83–40*; **G12**—Kentucky, Lyon Co., Buzzard Rock, along Cumberland River SE of Suwanee, *Gastony 83–42*; **G13**—Maryland, Washington Co., limestone cliffs near Dam 5 along Potomac River, *Gastony, 83–51*; **G14**—Missouri, Franklin Co., limestone cliffs from Fisher Cave to river, Meramec State Park, E of Sullivan, *Gastony 83–36*.

P. glabella var. *occidentalis*. **O1**—South Dakota, Pennington Co., 3.5 mi N of Deerfield, Flag Mt., rock crevices in open woods at top, *Gastony 83–63*; **O2**—South Dakota, Pennington Co., 6 mi S of Deerfield, S- to SW-facing limestone cliffs along Rte. 291, *Gastony 83–62*; **O3**—South Dakota, Lawrence Co., S- and SE-facing high cliffs above Hanna campground, ca. 2 mi SSE of Cheyenne Crossing, *Gastony 83–65*; **O4**—Wyoming, Crook Co., limestone outcrops along Rte. 863, 9.1 mi S of jct. Rte. 863 and I90 at Beulah, *Gastony 83–67*; **O5**—Wyoming, Washakie Co., cliffs and huge boulders lining Leigh Canyon off Rte. 16, *Gastony 83–70*; **O6**—Wyoming, Sheridan Co., limestone cliffs along Tongue River ca. 3.5 mi along Rte. 343 from jct. with Rte. 14, *Gastony 83–69*; **O7**—Wyoming, Bighorn Co., Bighorn Nat. Forest, limestone outcrops ca. 2 mi. NW of Tyrrell Ranger Station, *Gastony 83–71*; **O8**—Utah, Uintah Co., Ashley Nat. Forest, ca. 15 mi NW of Maeser, limestone outcrops in Brownie Canyon, *Gastony 83–72*.

P. glabella var. *glabella*, sexual diploid. **M1**—Missouri, Carter Co., SW-facing cliffs along Current River, S of Van Buren, *Gastony 83–41*; **M2**—Missouri, Jefferson Co., river bluffs 10 miles W of De-Soto, near jct. of road H and Big River, *Gastony 83–34*; **M3**—Missouri, Jefferson Co., bluffs along Big River on road Y, across road from Bethlehem Church, ca. 4 mi SE of Grubville, *Gastony 83–35*; **M4**—Missouri, Dent Co., limestone bluffs along Meramec River between Howe and Sligo, *Gastony 83–39*; **M5**—Missouri, Pulaski Co., Gasconade River at Rte. 7, between Richland and Lequey, on limestone cliff faces, *Gastony 82–27C*.

P. atropurpurea × *P. glabella* var. *occidentalis*, tetraploid hybrid. **HAO1**—Alberta, E-facing cliffs at S end of Barrier Lake S of Seebe, *Gastony 82–15*; **HAO2**—Wyoming, Crook Co., limestone outcrops along Rte. 863, 9.1 mi S of jct. Rte. 863 and I90 at Beulah, *Gastony 83–67*. **HAO3**—South Dakota, Pennington Co., ca. 10 mi W of Rapid City, limestone outcrops under pines along Rte. 44, *Gastony 83–64*.

P. atropurpurea × sexual *P. glabella* var. *glabella*, tetraploid hybrid. **HAM1**—Missouri, Dent Co., limestone bluffs along Meramec River between Howe and Sligo, *Gastony 83–39*.

Enzyme designations, electrophoretic procedures, and recipes for extraction buffer, gel and electrode buffers, and enzyme assays are as in Soltis et al. (1983). The Tris-HCl extraction buffer was used with PVP 40,000 at 2.5 g/25 ml. For all cited populations (Table 1) an average of 30 sporophytes were analyzed for 14 enzymes on each of the gel/electrode systems in Soltis et al. (1983) and on the Poulik discontinuous Tris-citrate and continuous Tris-citrate II systems of

Selander et al. (1971). Some of these enzymes did not resolve adequately on any of these systems. Of the enzymes that were well resolved, only those (PGM, PGI, TPI, SkDH, AAT, MDH) providing taxon-specific genetic markers for *Pellaea atropurpurea* and the *P. glabella* complex are considered here, because only these supply the most unequivocal data about the genomic ancestry of the derivative agamosporous tetraploid taxa. These six enzymes are coded by at least 10 loci (the genetic basis of the AAT patterns is uncertain), and in all cases the bands migrated anodally. When more than one isozyme was present for an enzyme, the most anodal isozyme was designated as "1," the next most anodal as "2," etc. Thus, isozymes and their coding genes are designated as in the following example: MDH-1 (the isozyme), *mdh-1* (the coding gene), MDH-2 (the isozyme), *mdh-2* (the coding gene).

The enzymes discussed and the gel-electrode systems (Soltis et al., 1983) on which they were resolved are: PGM, PGI, TPI on 7 (except in Fig. 8, TPI on 8); SkDH on 2; AAT on 10; MDH on 9. All gel slices were incubated in stains in the dark at 37° C. The number 7 gel was subjected to electrophoresis at 35 mamp for 6.5 hr until a bromphenol blue (BPB) marker dye reached 13.2 cm from origin; the number 10 gel, 35 mamp for 6 hr, BPB at 13.3 cm; the number 2 gel, 30 mamp for 6.5 hr, BPB at 13.8 cm; the number 9 gel, 35 mamp for 6 hr, BPB at ca. 13 cm. In all cases 13.2% starch concentration was used, electrophoresis was conducted at 4° C, and wicks were removed from the gels after 10 min. of electrophoresis at the indicated amperages, except that the numbers 2 and 10 gels were kept at 25 mamp until the wicks were removed.

Genetic interpretations of enzyme banding patterns in the sexually reproducing taxa are based on gametophytic segregational analyses as in Gastony and Gottlieb (1982). The banding patterns of agamosporous fern taxa do not segregate because of preferential pairing of sister chromosomes derived from the endomitotic division preceding meiosis in Döpp-Manton sporogenesis

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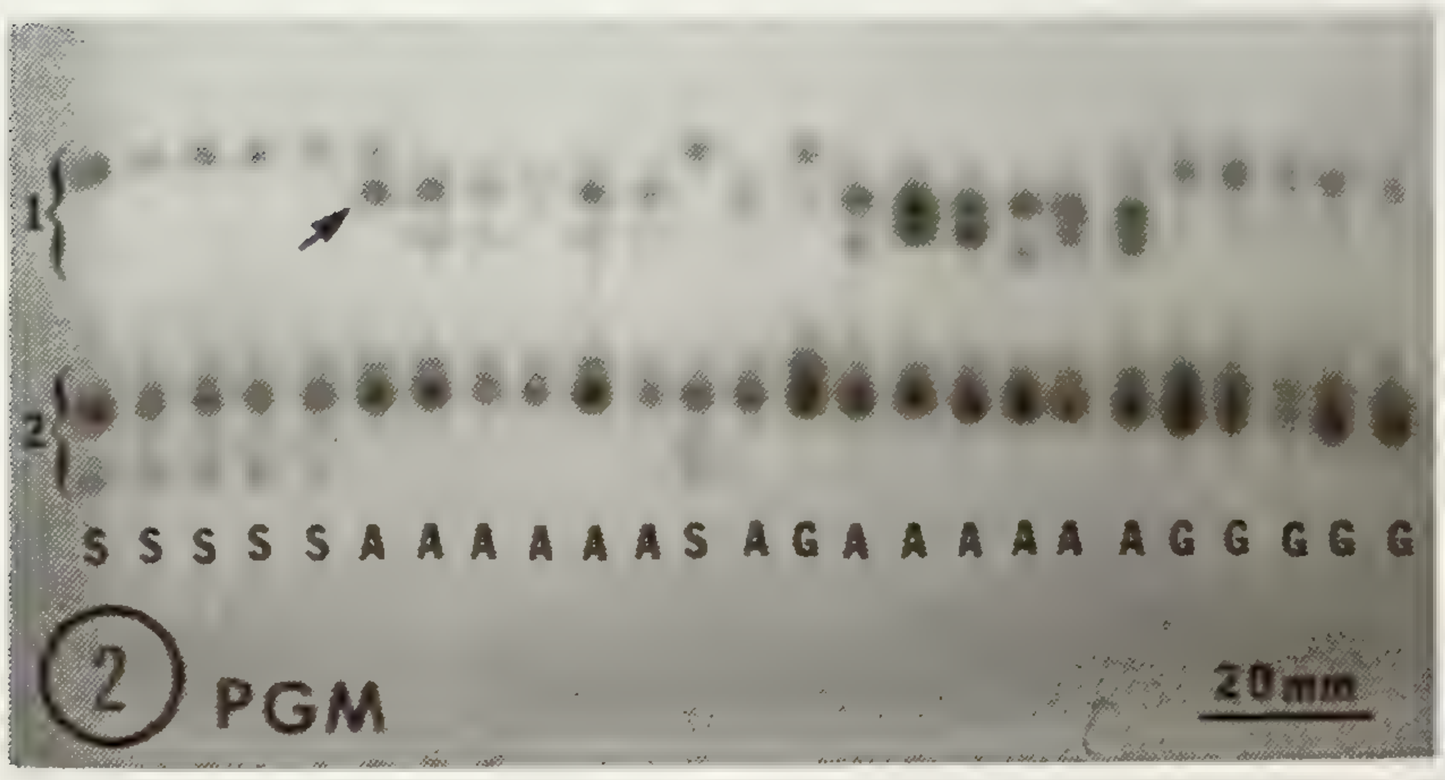
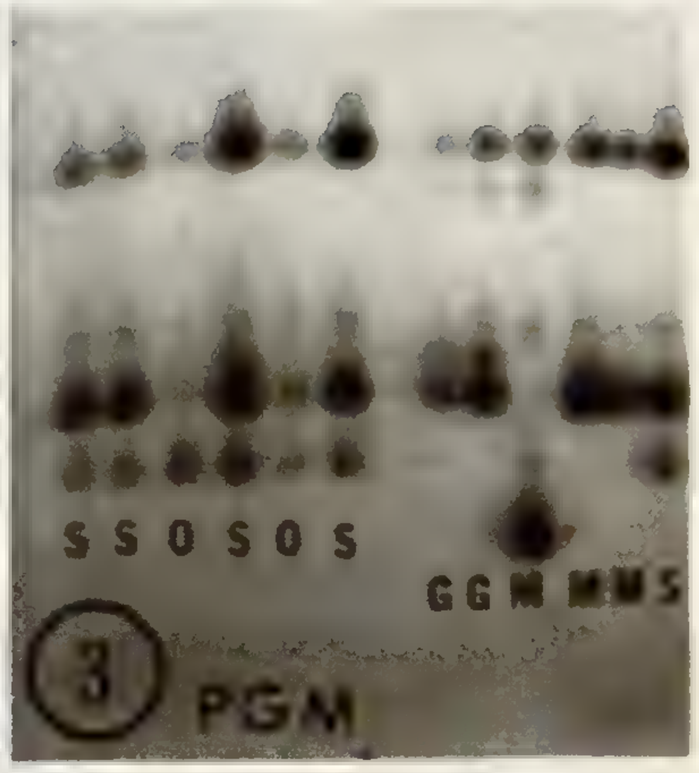
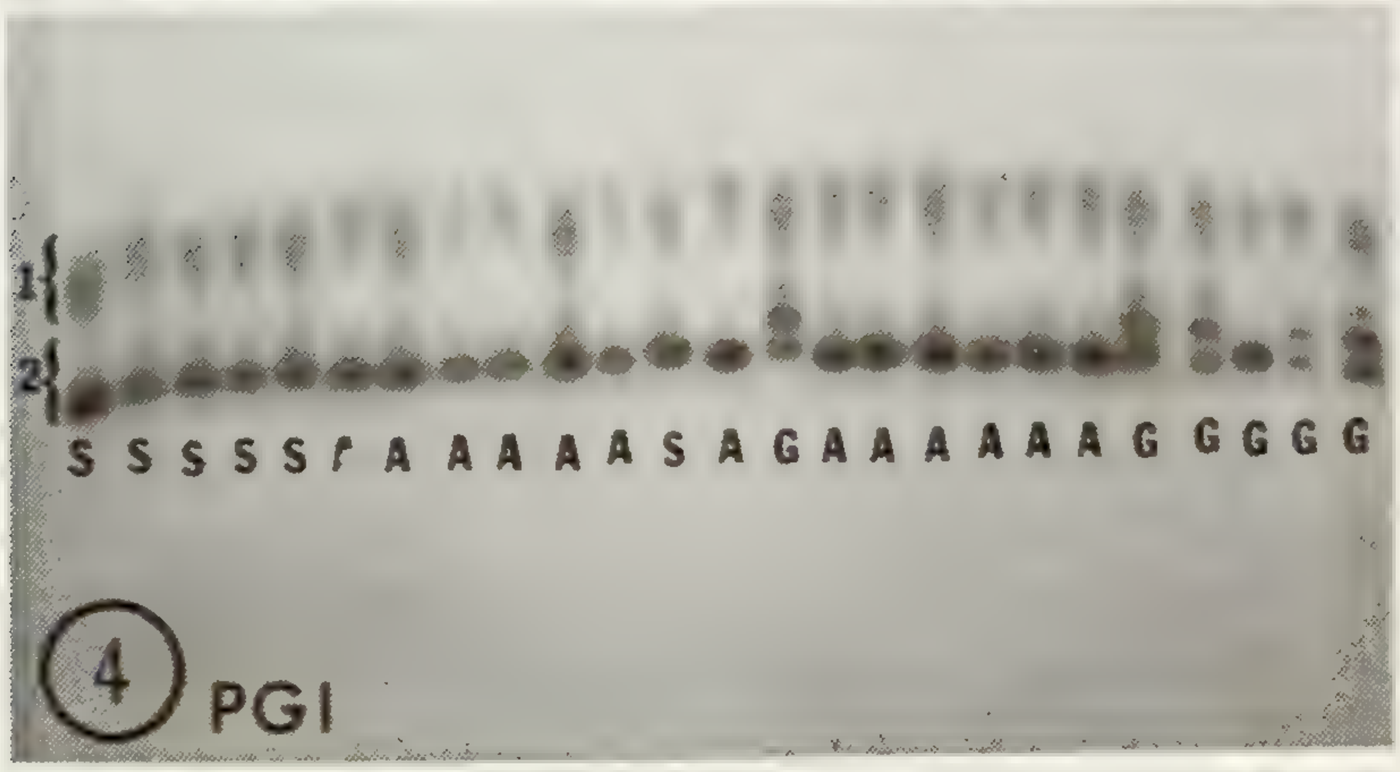
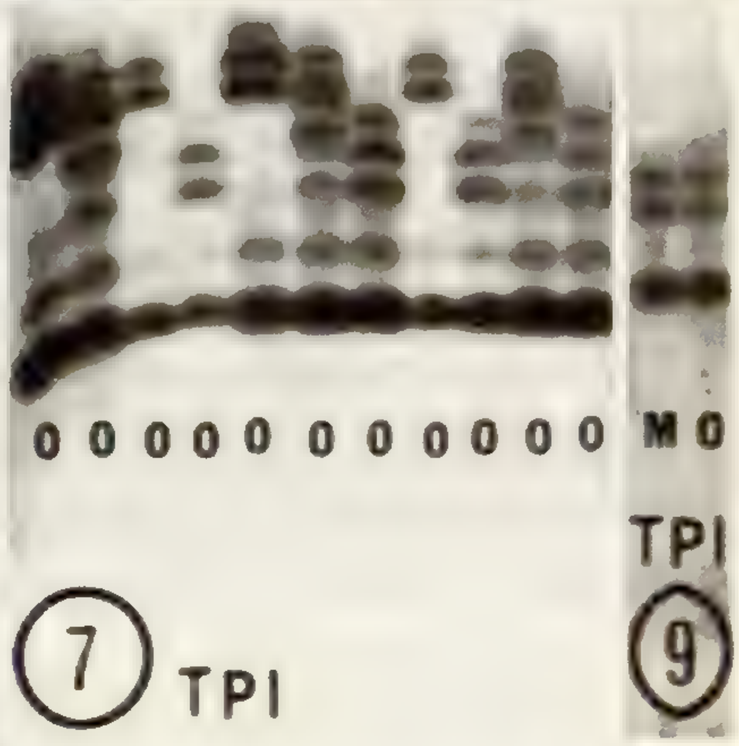
FIGS. 2–12. Electrophoretic banding patterns of the *Pellaea glabella* complex and *P. atropurpurea*. In all figures, the anode is toward the top and origin is at the bottom, except that the gel was cut two cm anodal to origin in Fig. 7 and one cm anodal to origin in Fig. 11. S = *P. glabella* var. *simplex*, O = var. *occidentalis*, G = agamosporous var. *glabella*, M = sexual var. *glabella*, A = *P. atropurpurea*. All lanes are from sporophytic tissue except where noted. See text for interpretation and discussion of the patterns. Millimeter bar in Fig. 2 represents a reduction factor of 0.5 for Figs. 2–12. FIGS. 2, 4, 6 have identical plant sequences as follow (acronyms of source populations as in Table 1): **lane 1** = S1; **2** = S2; **3** = S3; **4** = S4; **5** = S5; **6** = A1; **7** = A2; **8** = A3; **9** = A4; **10** = A5; **11** = A6; **12** repeats S3; **13** repeats A4; **14** = G1; **15** = A7; **16** = A8; **17** = A9; **18** = A10; **19** = A11; **20** = A12; **21** = G2; **22** = G3; **23** = G4; **24** = G5; **25** repeats G1. FIG. 3: **lane 1** = S1; **2** = S5; **3** = O1 pooled gametophytes; **4** repeats 1; **5** = O5 pooled gametophytes; **6** repeats 1; **7** = G2; **8** = G1; **9** = M1; **10** = M1; **11** = M2; **12** repeats 1. FIG. 5: **lane 1** = S6; **2** = S2; **3** = S4; **4** = S5; **5** = O1; **6** repeats 4; **7** = M4; **8** = M5; **9** = M2; **10** = M1; **11** repeats 4; **12** = G7; **13** = G8; **14** = G4; **15** repeats 7; **16** = O3; **17** = G9; **18** repeats 9; **19** = G2; **20** = G10; **21** = G10; **22** = G6. FIG. 7: **lane 1** = O2; **2** = O8; **3, 4, 8, 9** = single gametophytes from sporophyte in lanes 2, 6, 10; **5** repeats 1; **6** repeats 2; **7** = O7; **10** repeats 2; **11** repeats 7. FIG. 8: **lane 1** = S1; **2** = S5; **3** = G2; **4** = G1; **5** repeats 1; **6** repeats 2; **7** = M4; **8** = O4; **9** = O6; **10** repeats 7; **11** = M4; **12** = M2; **13** repeats 8; **14** repeats 1; **15** repeats 2; **16** repeats 9. FIG. 9: **lane 1** = M1; **2** = O5. FIG. 10: **lane 1** = M2; **2** = G2; **3** = O7; **4** = O5; **5** = M4; **6** = S5. FIG. 11: **lane 1** = O5; **2** = S6; **3** = O8. FIG. 12: **lane 1** = S6; **2** = S2; **3** = O5; **4** = O8; **5** = O5; **6** = G5; **7** = G4.

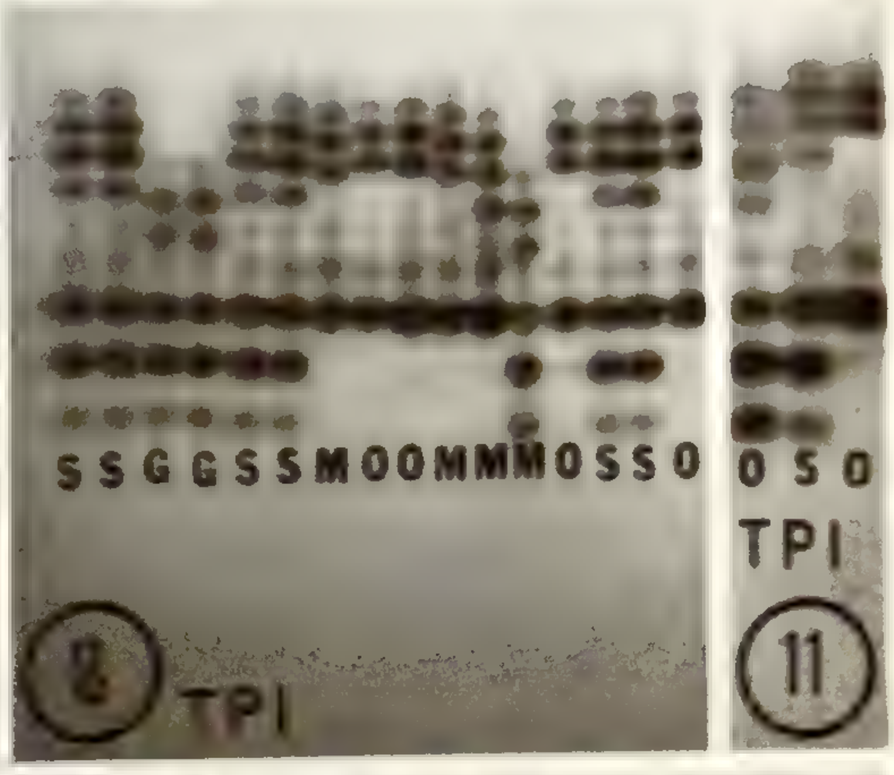

1
2
S S S S S A A A A A S A G A A A A A G G G G G
2 PGM
20mm

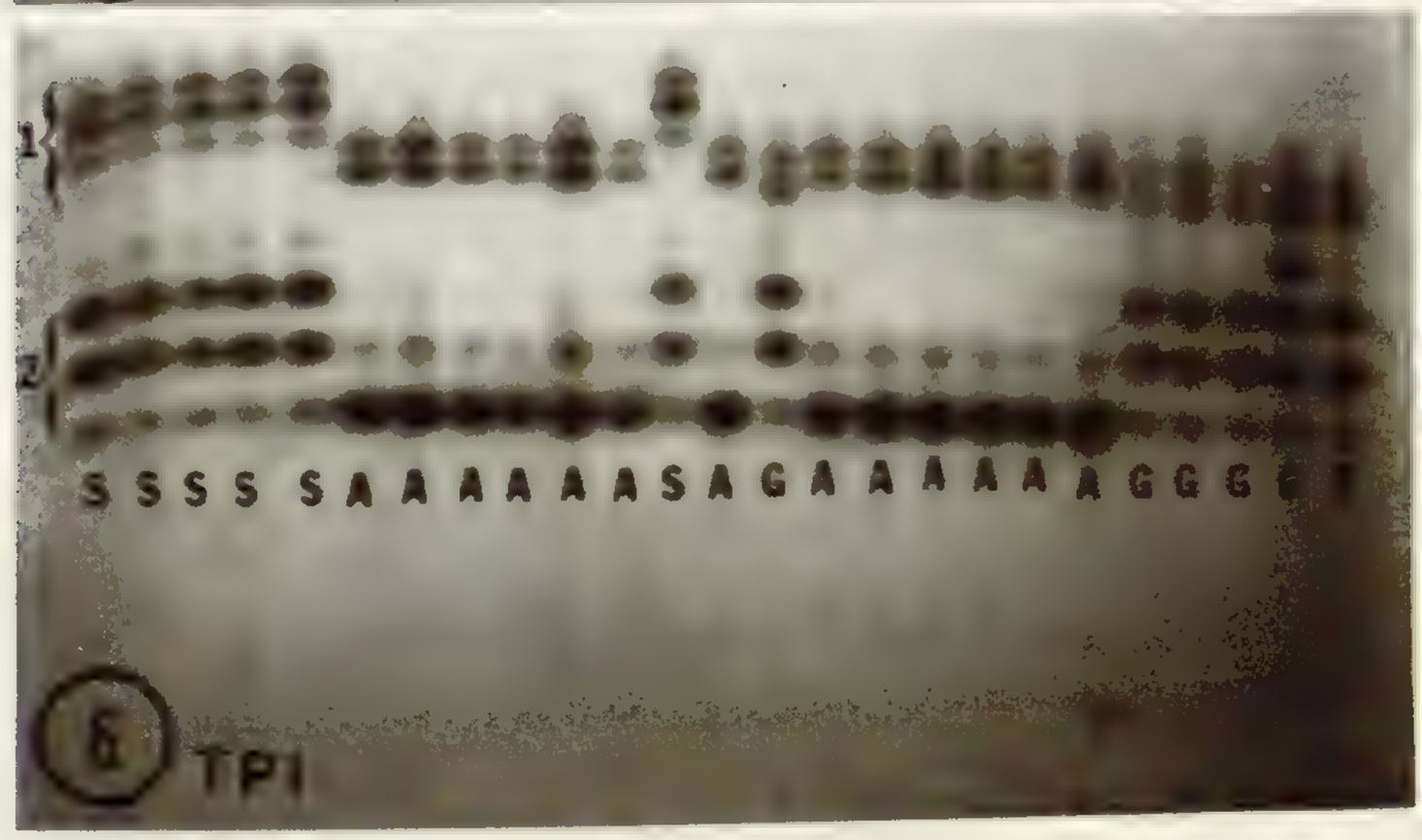

S S O S O S
G G M M M S
3 PGM


1
2
S S S S S r A A A A S A G A A A A A G G G G G
4 PGI


O O O O O O O O O O O O
M O
TPI
7 TPI
9

S S S S O S M M M M S G G G M O G M G G G G
5 PGI


S S G G S S M O O M M M O S S O
O S O
TPI
8 TPI
11


1
2
S S S S S A A A A A A S A G A A A A A A G G G G
6 TPI

M G O O M S
10 TPI

S S O O O G G
12 TPI

(Gastony & Gottlieb, 1985). Thus even heterozygous patterns are fixed in the agamosporous taxa examined here, and their genetic interpretations are inferred by comparison with the co-migrating patterns of sexual taxa subjected to side by side electrophoresis on the same gels.

Results

The three agamosporous taxa each have unique banding patterns for the monomeric enzyme PGM (Fig. 2). This enzyme occurs as two isozymes, one in the cytosol and a second in the chloroplasts (Gottlieb, 1981; Weeden, 1983; Gastony & Darrow, 1983). As shown in Fig. 2, var. *simplex* (lanes S) expresses a single PGM-1 band. *Pellaea atropurpurea* (lanes A) expresses several two-banded patterns at PGM-1, all with one of the bands at the position indicated by the arrow in Fig. 2. In lane 6, the second PGM-1 band is co-migratory with the single PGM-1 band in var. *simplex*, but in most cases the second band occupies one of two slower positions (lanes 7–11, 13, 15–20). Tetraploid *P. glabella* var. *glabella* (lanes G) is two-banded at PGM-1, with a relatively strong band co-migratory with the single band in var. *simplex* and a slower weaker band apparently co-migratory with the invariant PGM-1 band (arrow) in *P. atropurpurea*. Banding intensities at PGM-1 in tetraploid *P. glabella* var. *glabella* suggest three doses of the allele coding the faster allozyme and a single dose of the allele coding the slower allozyme. Note that the triploid genotypes coding observed PGM-1 patterns in sampled populations of *P. atropurpurea* could not be added to any haploid genotype to yield the tetraploid PGM-1 banding patterns of vars. *simplex* or *glabella*.

At PGM-2 (Fig. 2), tetraploid var. *simplex* (lanes S) has a two-banded pattern whose unequal staining intensities suggest three doses of the allele coding the stronger and faster allozyme and a single dose of the allele coding the weaker and slower allozyme. The tightly two-banded pattern of tetraploid var. *glabella* (lanes G) also suggests three doses of the allele coding the slightly slower allozyme that comigrates with the stronger allozyme of var. *simplex* (compare lanes 12 and 14), and a single dose of the allele coding the slightly faster allozyme. *Pellaea atropurpurea* (lanes A) is single-banded, implying that its triploid genotype is fixed for the allele coding the same allozyme that is dominant in the other two taxa (compare lanes 12–14). Thus all three taxa appear to share three doses of the same allele at PGM-2, so that this locus cannot be used to exclude *P. atropurpurea* from the ancestry of the tetraploid varieties.

Representative banding patterns of PGM in agamosporous varieties *simplex* and *glabella* are compared to the patterns of the sexual taxa in Fig. 3. In var. *simplex* (lanes S), single-banded PGM-1 and two-banded PGM-2 are comigratory with the apparently homologous allozymes of sexual var. *occidentalis* (lanes O, both lanes representing randomly selected pooled gametophtyes derived from the spores of heterozygous sporophytes). Thus all PGM bands in var. *simplex* are found in var. *occidentalis* and can therefore be accounted for by loci and alleles inherited entirely from var. *occidentalis*. Lanes G show the two-banded patterns for both PGM-1 and PGM-2 in agamosporous var. *glabella*. The faster (more intense) band at PGM-1 is found in sexual var. *glabella* (lanes M), but this is not

instructive since it is common to both agamosporous and both sexual taxa of *P. glabella*. The slower (less intense) band at PGM-1 in agamosporous var. *glabella* distinguishes that taxon from var. *simplex* which lacks it. That slower band has not been found in any sporophyte of var. *occidentalis* examined but has been observed in two sporophytes of sexual var. *glabella* (e.g., lane 9). At PGM-2, agamosporous var. *glabella* (lanes G) is two-banded. The slower band is found in all *glabella* taxa, including sexual var. *glabella* (lanes 10, 11). The faster band has not yet been found in sexual var. *glabella* or in var. *occidentalis*. Its coding allele may now be either very rare in the sexual progenitor or lost from it, leaving it as an orphan allele in the tetraploid, similar to the orphan alleles encountered by Werth et al. (1985) in their study of polyploid *Asplenium* taxa.

The dimeric enzyme PGI exhibits two isozymes, one active in the cytosol and a second in the chloroplasts (Gottlieb, 1981; Weeden, 1983). PGI-1, the putatively chloroplastic isozyme (Gastony & Darrow, 1983), did not resolve into bands (Fig. 4) and will not be discussed. PGI-2 (Fig. 4) is single-banded in *P. glabella* var. *simplex* (lanes S), *P. atropurpurea* (lanes A), and certain populations of agamosporous *P. glabella* var. *glabella* (lane 23). In most populations of the latter, PGI-2 has a three-banded pattern of asymmetric intensities (lanes 14, 21, 22, 24, 25), suggesting that these tetraploids have 3 doses of the allele coding the slower allozyme and a single dose of the allele coding the faster allozyme, with the central heterodimeric band nearly equalling the slow homodimeric band in intensity. The single PGI-2 band of var. *simplex* is co-migratory with the single band or the most cathodal band of var. *glabella* (compare lanes 12, 14), but the nearly co-migratory single band of *P. atropurpurea* (lane 13) is slightly slower. This lesser migration of PGI-2 in *P. atropurpurea* is subtle, but it has been confirmed many times in gels with various juxtapositions of these taxa. Although this distinction might not be convincing of itself, it gains strength from its correlation with distinctions based on other enzymes. Thus inasmuch as PGI-2 in *P. atropurpurea* does migrate to a position slightly cathodal to the analogous PGI-2 bands in the *P. glabella* complex, the triploid PGI-2 genotype of *P. atropurpurea* cannot be a constituent of the genotypes of the agamosporous tetraploids.

Figure 5 shows that the invariant one-banded pattern for PGI-2 in var. *simplex* (lanes S) is identical to the invariant one-banded pattern of this isozyme in sexual var. *occidentalis* (lanes O). In hundreds of specimens of var. *occidentalis* from throughout its range, all sporophytes expressed this same single band for PGI-2. Figure 5 also shows that this same band is found in sexual var. *glabella* (most lanes M) and agamosporous var. *glabella* (lanes G). The more anodal homodimeric allozyme seen in those populations of agamosporous var. *glabella* characterized by a three-banded PGI-2 pattern (lanes 17, 19, 21, 22) is frequently observed in sexual var. *glabella* (e.g., lanes 8, 9, 18) but never observed in hundreds of sporophytes throughout the range of var. *occidentalis*, suggesting that the allele for this allozyme in agamosporous var. *glabella* came from sexual var. *glabella*.

Dimeric TPI is also expressed as cytosolic and chloroplastic isozymes in plants (Gottlieb, 1981; Pichersky & Gottlieb, 1983). One zone of TPI activity

appears as a non-segregating, asymmetrically stained, three-banded pattern in homozygous plants of nearly all fern species examined. This is usually the more anodally migrating zone (TPI-1), and this three-banded pattern has been attributed to either a single gene duplication or a post-translational modification (Gastony & Darrow, 1983; Gastony & Gottlieb, 1985; Haufler, 1985; Haufler et al., 1985; Gastony, 1986; Haufler & Soltis, 1986; Soltis, 1986; Soltis & Soltis, 1986). Post-translational charge modification of some of the coded TPI-1 protein is the more probable explanation (see Appendix, p. 66). When the locus coding this pattern is heterozygous, it codes 10 enzyme bands (four homodimers and six heterodimers), but these usually appear as a four-banded to seven-banded pattern depending on the number of overlapping or nearly overlapping bands and on the faintness of the anodal homodimers.

From Fig. 6 it is clear that var. *simplex* (lanes S) is fixed for a heterozygous five-banded pattern at TPI-1 (the slowest band being quite faint) whereas agamosporous var. *glabella* (lanes G) and *P. atropurpurea* (lanes A) are invariant for their respective asymmetrical three-banded patterns. Several side-by-side comparisons among these TPI-1 patterns on different gels have shown that the bands of *P. atropurpurea* are not co-migratory with those of var. *simplex* nor with those of var. *glabella*. Therefore the triploid TPI-1 pattern of *P. atropurpurea* could not be added to any haploid TPI-1 pattern to yield the tetraploid TPI-1 patterns of *P. glabella* vars. *simplex* and *glabella*.

Sporophytes of var. *occidentalis* homozygous at *tpi-1* express either of two three-banded patterns (Fig. 7, lanes 5, 7) while the comparable heterozygote (lane 6) shows several additional heterodimeric bands (seven of the ten expected bands are fairly easily distinguished in this gel that was run extra long to maximize band separation), and lanes 3, 4, 8 and 9 show segregation of the constituent homozygous 3-banded patterns in single gametophytes derived from the heterozygous sporophyte in lanes 2, 6, and 10. Similarly, sporophytes of sexual var. *glabella* homozygous at *tpi-1* express either of two three-banded patterns (Fig. 8, lanes 10, 12), while a sporophtye heterozygous at this locus (lane 11) expresses a five-banded pattern on this gel system (because of comigration of some of the bands). The slower three-banded TPI-1 patterns of var. *occidentalis* and sexual var. *glabella* are identical (Fig. 9; Fig. 10, compare lanes 1, 3). As seen in Fig. 8, lanes 7–10, however, the faster three-banded TPI-1 pattern of sexual var. *glabella* is not identical to that of var. *occidentalis*, but rather all three bands of sexual var. *glabella* (lanes 7, 10) are slightly slower than their counterparts in var. *occidentalis* (lanes 8, 9).

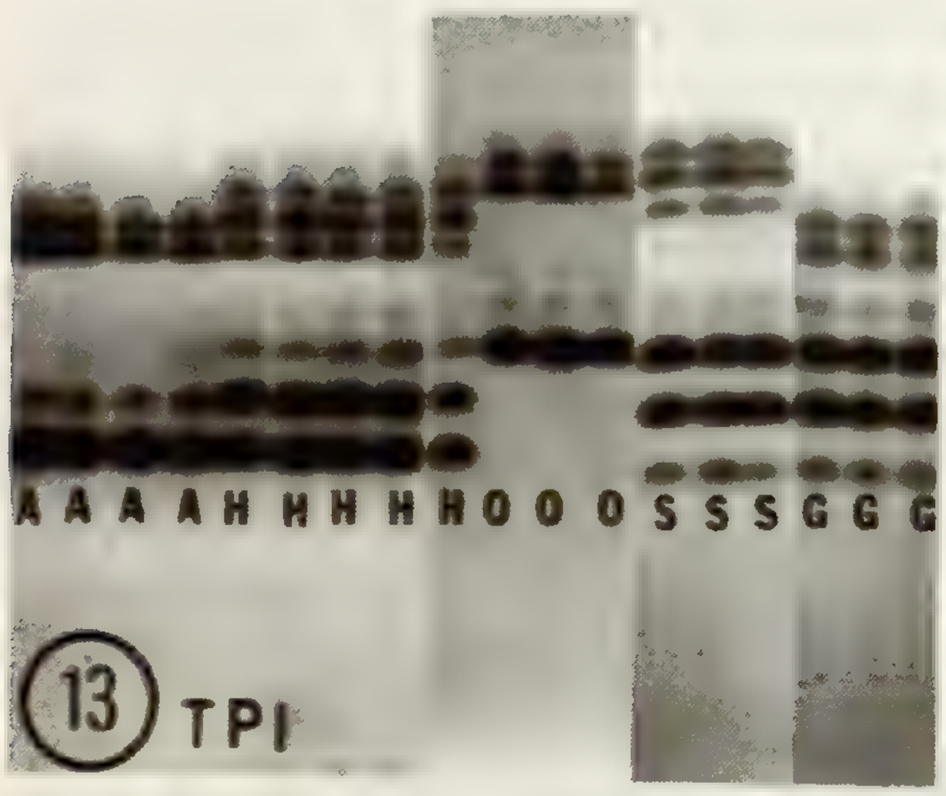
The characteristic TPI-1 banding patterns of var. *simplex* and agamosporous var. *glabella* inconsistent with a derivation from *P. atropurpurea* are consistent with derivations from var. *occidentalis* and sexual var. *glabella*. All sampled populations of agamosporous var. *glabella* [except the outlier in Texas (Fig. 1)] are characterized by a three-banded pattern at TPI-1 (e.g., Fig. 10, lane 2). These bands are identical to those of the slower three-banded TPI-1 pattern common to sexual var. *glabella* (Fig. 10, lane 1) and sexual var. *occidentalis* (Fig. 10, lane 3). Thus the data from TPI-1 are consistent with an origin of agamosporous var. *glabella* from either of these sexual taxa. As seen in Fig. 8, lanes 14, 15, var.

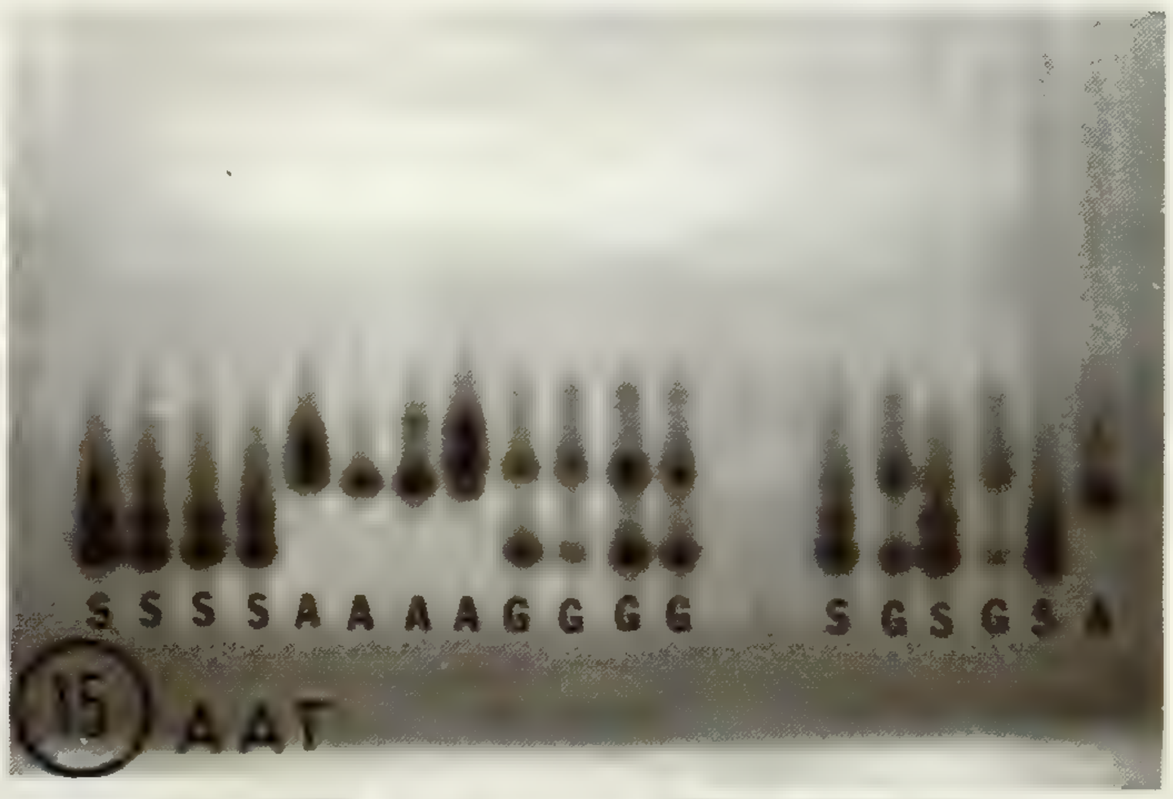
simplex exhibits five bands, of which the three anodal bands align perfectly with those of var. *occidentalis* (lanes 13, 16) and in lanes 5, 6 do not align with those from sexual var. *glabella* (lane 7). The slower TPI-1 bands in var. *simplex* are faint as would be expected if three doses of the faster pattern of TPI-1 from var. *occidentalis* were combined with a single dose of the slower pattern of TPI-1 shared by the sexuals, as seen by comparing lanes 4, 6 of Fig. 10. Under this interpretation, the slowest strong TPI-1 band in var. *simplex* (lane 6) should be the heterodimer between the cathodal homodimers of the faster and slower three-banded TPI-1 patterns. Figure 11 shows that the slowest strong TPI-1 band in var. *simplex* (lane 2) does correspond to that heterodimeric band in the heterozygous TPI-1 pattern of diploid var. *occidentalis* (lane 1) which has equal doses of the *tpi-1* alleles. That this band is truly heterodimeric in var. *occidentalis* is established by comparing lanes 5–7 of Fig. 7 where the heterozygote is flanked by respective homozygotes.

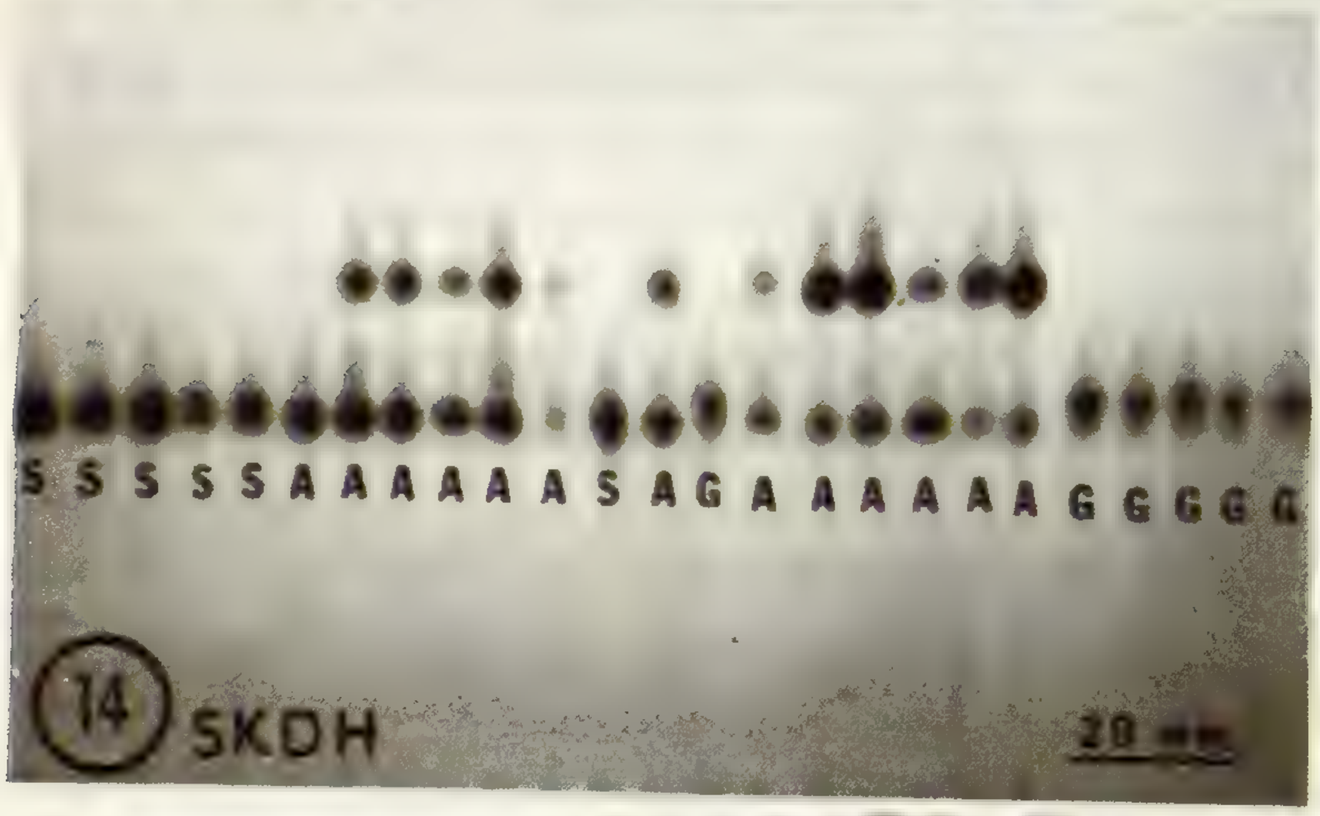
At TPI-2 (Fig. 6), var. *simplex* (lanes S) and agamosporous var. *glabella* (lanes G) exhibit the same asymmetrical three-banded pattern, suggesting that they are fixed for three doses of the allele coding the faster homodimer and one dose of the allele coding the slower homodimer. The population of var. *glabella* represented by the second-last lane is strongly banded between TPI-2 and TPI-1 where other populations exhibit only a very faint band taken to reflect post-translationally modified protein. The TPI-2 pattern of *P. atropurpurea* (lanes A) is invariant and probably best interpreted as intensely single-banded with the faint anodal band representing post-translationally modified protein. The strong TPI-2 band of *P. atropurpurea* is co-migratory with the slower (fainter) homodimeric band of vars. *simplex* and *glabella* on several gel-electrode systems. The genotype coding this locus in triploid *P. atropurpurea* sampled in this study, however, could not combine with any haploid genotype to produce the relative staining intensities of the TPI-2 bands of tetraploid vars. *simplex* and *glabella*. The validity of this reasoning can be established by examining the TPI-2 patterns of true hybrids between *P. atropurpurea* and the sexual taxa. Because such hybrids would be tetraploid with three genome doses contributed by the triploid sperm of *P. atropurpurea*, their morphological intermediacy should be strongly skewed toward this triploid parent. The relative intensities of the bands of the additive enzyme patterns of true hybrids should also reflect the 3:1 *atropurpurea*: sexual-parent gene dosages. Occasional tetraploid plants (verified by chromosome counts) matching these morphological expectations have been encountered in Alberta, Wyoming, South Dakota, and Missouri where the ranges of these taxa overlap. As an example, composite Fig. 13 presents TPI banding patterns of these hybrid sporophytes (lanes H) in comparison with the patterns of parental *P. atropurpurea* (lanes A) and var. *occidentalis* (lanes O). Figure 13 also compares the TPI patterns of these true hybrids (lanes H) with those of var. *simplex* (lanes S) and agamosporous var. *glabella* (lanes G). The maternal parent (not shown) of the hybrid from Missouri (lane 7) is sexual var. *glabella* with the faster allozyme at both TPI-1 and TPI-2. The observed enzyme additivity and staining intensities of these true hybrids are in precise agreement with expectations and

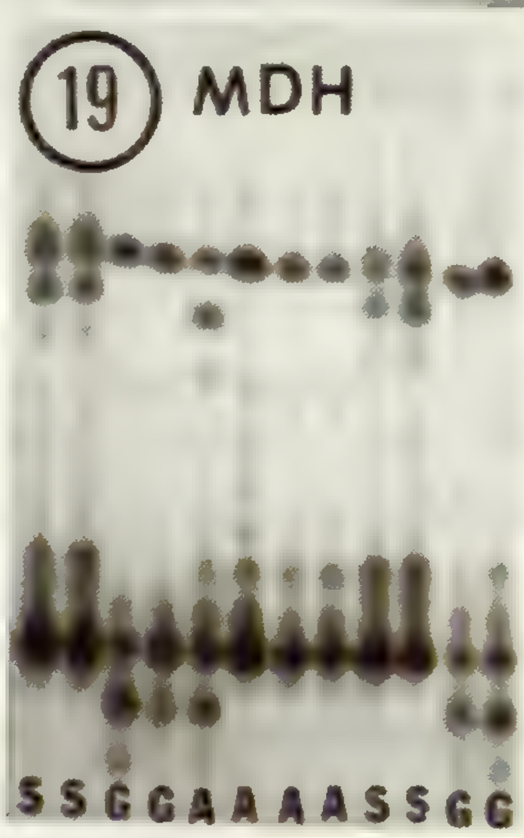
do not match the relative band intensity patterns of agamosporous tetraploid vars. *simplex* and *glabella*.

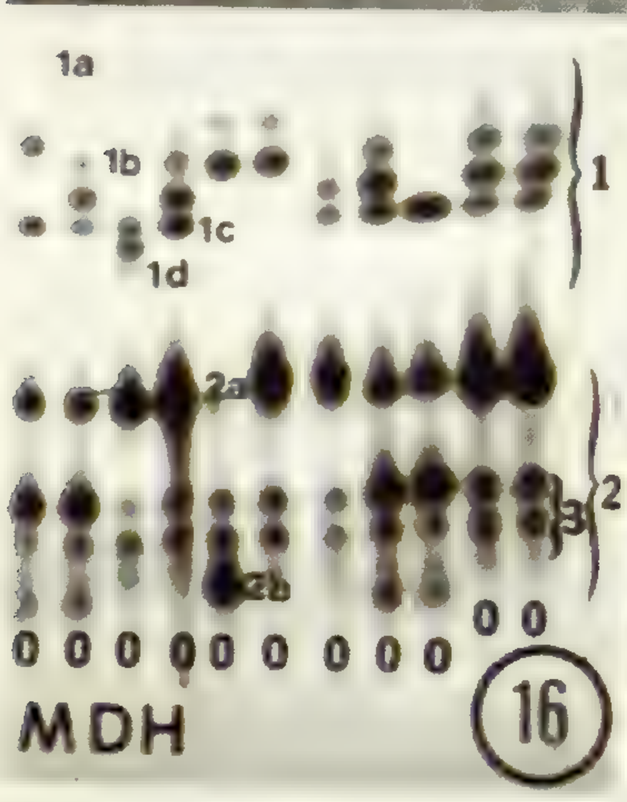
Both *tpi-2* alleles coding the homodimeric TPI-2 bands in var. *simplex* (Fig. 8, lanes S) and agamosporous var. *glabella* (Fig. 8, lanes G) are found in sexual var. *glabella* (Fig. 8, lanes M) and in var. *occidentalis* (Fig. 12, lanes O; compare lane 3 with var. *simplex* in lanes S and with agamosporous var. *glabella* in lanes G). Because both agamosporous taxa and both sexual taxa carry the same *tpi-2* alleles, data from this locus are not useful in defining specific progenitor-derivative pairs, although they are consistent with the autopolyploid derivations indicated by other isozymes.

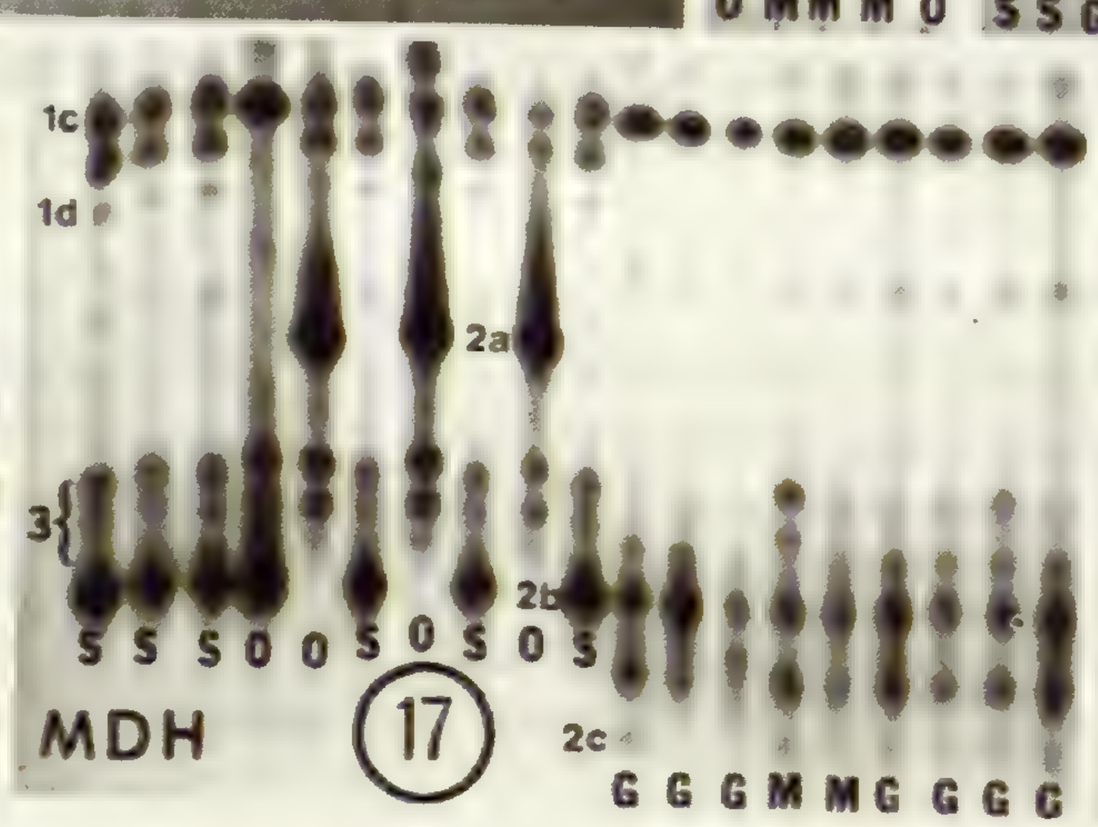












For the monomeric enzyme SkDH (Fig. 14), var. *simplex* (lanes S) expresses a very tightly grouped two-banded pattern in which the two contiguous bands are of equal intensity. Agamosporous var. *glabella* (lanes G) is also tightly two-banded and the bands are aligned with those in var. *simplex*, but the more anodal is about three times more intense than the cathodal. In *P. atropurpurea* (lanes A), SkDH is almost always expressed as two well separated bands, the exception seen here being the population from Arizona (lane 6) where a single band is expressed. The more cathodal of the two bands in *P. atropurpurea* appears to be co-migratory with the more cathodal band in vars. *simplex* and *glabella*. In most two-banded populations of *P. atropurpurea* the cathodal band is more intense than the anodal (lanes 7–11, 13, 15, 18) suggestive of a two to one gene dosage effect in this triploid taxon. In four of the populations analyzed (lanes 16, 17, 19, 20), however, the band intensities are just the opposite, with the anodal band approximately twice the intensity of the cathodal. Agamosporous vars. *simplex* and *glabella* lack the anodal band of most populations of *P. atropurpurea* and their cathodal allozyme is less intense than would be expected if they inherited it from triploid *P. atropurpurea* with the single-banded pattern in lane 6. Thus SkDH further decreases the probability that the genome of *P. atropurpurea* is a component of the genomes of the agamosporous tetraploids. Both bands of var. *simplex* are found in var. *occidentalis* where their tightly grouped two-banded pattern in heterozygotes has been shown to segregate in gametophytes. Only the stronger, more anodal of the two bands in agamosporous var. *glabella* has been observed in sexual var. *glabella*.

AAT is a dimeric enzyme with one to four isozymes reported from plants (Gottlieb, 1981, 1982). The distinctive three-banded patterns of var. *simplex* (Fig. 15, lanes S) and var. *glabella* (lanes G) sharply differentiate them, although their most cathodal bands are co-migratory (lanes 13–17). Three AAT patterns are expressed by the 12 populations of *P. atropurpurea* analyzed for AAT, two

←

FIGS. 13–20. Electrophoretic banding patterns of the *Pellaea glabella* complex and *P. atropurpurea*. In all figures, the anode is toward the top and origin is at the bottom, except that the gel was cut 0.5 cm anodal to origin in Figs. 16, 17. S = *P. glabella* var. *simplex*, O = var. *occidentalis*, G = agamosporous var. *glabella*, M = sexual var. *glabella*, A = *P. atropurpurea*. See text for interpretation and discussion of the patterns. Millimeter bar in Fig. 14 represents a reduction factor of 0.5 for Figs. 13–20. In composite FIG. 13: **lane 1** = A1; **2** = A4; **3** = A12; **4** = A14; **5** = HAO1; **6** repeats 5; **7** = HAM1; **8** = HAO3; **9** = HAO2; **10** = O3; **11** = O5; **12** = O5; **13** = S2; **14** = S3; **15** = S4; **16** = G12; **17** = G8; **18** = G13. FIG. 14: **lane 1** = S1; **2** = S2; **3** = S3; **4** = S4; **5** = S5; **6** = A1; **7** = A2; **8** = A3; **9** = A4; **10** = A5; **11** = A6; **12** repeats S3; **13** repeats A4; **14** = G1; **15** = A7; **16** = A8; **17** = A9; **18** = A10; **19** = A11; **20** = A12; **21** = G2; **22** = G3; **23** = G4; **24** = G5; **25** repeats G1. FIG. 15: **lane 1** = S1; **2** = S2; **3** = S5; **4** = S4; **5** = A1; **6** = A13; **7** = A7; **8** = A12; **9** = G2; **10** = G3; **11** = G4; **12** = G6; lanes 13–18 test band alignments of all three taxa—**13** repeats 2; **14** repeats 9; **15** repeats 2; **16** repeats 10; **17** repeats 3; **18** repeats 7. FIG. 16: **lane 1** = O5; **2** = O7; **3** = O5; **4** = O5; **5** = O7; **6** = O7; **7** = O7; **8** = O8; **9** = O5; **10** = O5; **11** = O5. FIG. 17: **lane 1** = S1; **2** = S2; **3** = S5; **4** = O6; **5** = O6; **6** repeats 1; **7** = O6; **8** repeats 1; **9** = O6; **10** repeats 1; **11** = G2; **12** = G1; **13** = G5; **14** = M1; **15** = M1; **16** repeats 11; **17** = G12; **18** = G7; **19** = G4. FIG. 18: **lane 1** = O1; **2** = M5; **3** = M5; **4** = M5; **5** = O1. FIG. 19: **lane 1** = S1; **2** = S2; **3** = G4; **4** = G1; **5** = A15; **6** = A16; **7** = A17; **8** = A7; **9** = S5; **10** = S4; **11** = G12; **12** = G7. FIG. 20: **lane 1** = M1; **2** = M1; **3** = G5; **4** = G6; **5** = G11; **6** = G7; **7** = M1; **8** = M5.

different three-banded patterns (lanes 5, 8) and a more commonly encountered pattern consisting of a single strong band (lane 6) sometimes with a less intense band anodal to it (lane 7). The anodal band in var. *simplex* appears to align with the most cathodal of the three *P. atropurpurea* bands in lane 5, but otherwise all observed patterns of *P. atropurpurea* differ so strongly from those of the other two taxa that the triploid genome coding these patterns in *P. atropurpurea* could not constitute three-fourths of the AAT genotype of the tetraploid varieties. Lack of variation for this enzyme in the sexual taxa and lack of segregation in agamosporous taxa preclude genetic interpretation of AAT banding patterns in this complex. Both sexual taxa exhibit the same two strong bands and these align with the most anodal and cathodal bands of var. *simplex*, whose central band may be heterodimeric. In addition, fainter, more anodal bands are evident in some plants of sexual var. *glabella*. However these do not align with the most anodal band usually visible in agamosporous var. *glabella*, so that the allele or gene coding that band is apparently orphaned. The unclear interpretation of AAT isozymes in this complex decrease the effectiveness of AAT for purposes of this paper, except that the AAT patterns of *P. atropurpurea* and the agamosporous tetraploids are strongly differentiated and strengthen arguments from other enzymes against the involvement of *P. atropurpurea* in the derivations of the tetraploids.

MDH is a dimeric enzyme usually expressed as 3 or more isozymes in plants (Gottlieb, 1981). In var. *occidentalis*, gametophytic segregation studies (as in Gastony & Gottlieb, 1982) demonstrate that the MDH-1 patterns in Fig. 16 are specified by four alleles coding allozymes 1a, 1b, 1c, 1d. Other "bands" seen at MDH-1 in this figure are post-translational artifacts. MDH-2 is expressed as allozymes 2a (seen in homozygous condition in lanes 3, 4, 6, 7, 10, 11) and 2b (homozygously expressed in lane 5). MDH-3 is a fixed (non-segregating) three-banded pattern best seen in lanes 3, 4, 6, 7, 10, 11. This pattern is either coded by a gene and its modified duplication or by post-translational modification of some of the coded protein as in the case of TPI-1. The most cathodal (slowest) band of this three-banded MDH-3 pattern is faint. Under the electrophoretic conditions expressed in this figure, MDH-2b overlaps the faint MDH-3 band when its coding allele *mdh-2b* is homozygous (lane 5). MDH-2b is seen slightly cathodal to this faint MDH-3 band when *mdh-2b* is heterozygous with *mdh-2a* (and allozyme 2b is therefore less intense; lanes 1, 2, 8, 9) or when the duration of electrophoresis is increased. When *mdh-2* is heterozygous, the heterodimer overlaps the most anodal of the MDH-3 bands (lanes 1, 2, 8, 9).

Three MDH isozymes also characterize sexual var. *glabella*. MDH-1 is invariantly single-banded (Fig. 17, lanes M), and aligns with allozyme 1c of var. *occidentalis* (lanes 4, 5, 9). Sexual var. *glabella* expresses one MDH-2 allozyme that corresponds to MDH-2b of var. *occidentalis* (Fig. 17, compare lanes M with lane 4) and an additional more cathodal allozyme absent from var. *occidentalis*. This slower MDH-2 allozyme of sexual var. *glabella* (MDH-2c) is seen in homozygous condition in Fig. 18 lanes M and in heterozygous condition (with heterodimer) in Fig. 17 lanes M. The three-banded MDH-3 pattern of sexual var. *glabella* is the same as in var. *occidentalis* (Fig. 18, compare lanes M with lane 5).

The agamosporous varieties of *P. glabella* are easily distinguished by their respective, invariant MDH patterns. Variety *simplex* (Fig. 17, lanes S) has a fixed three-banded pattern at MDH-1, the same fixed three-banded MDH-3 pattern seen in the sexual taxa, and a single intense MDH-2b band cathodal to MDH-3. Agamosporous var. *glabella* (Fig. 17, lanes G) has a single intense MDH-1c band aligned with the most anodal MDH-1 band of var. *simplex*, the same three-banded MDH-3 pattern as the other members of this complex, and a fixed three-banded MDH-2 pattern just cathodal to three-banded MDH-3. The most anodal MDH-2 band in agamosporous var. *glabella* (Fig. 17, lane 11) aligns with the MDH-2b band in var. *simplex* (Fig. 17, lane 10), whereas the most cathodal band in lane 11 aligns with MDH-2c of sexual var. *glabella* (lanes M).

Sporophytes of *P. atropurpurea* examined for MDH (Fig. 19, lanes A) express the MDH-1 allozyme shared by all taxa of the *P. glabella* complex and may express additional MDH-1 allozymes not relevant to the agamosporous taxa of the *glabella* complex (e.g., Fig. 19, lane 5). At MDH-3, *P. atropurpurea* expresses the same fixed three-banded pattern as all the *P. glabella* taxa. At MDH-2, *P. atropurpurea* has either a single band (Fig. 19, lanes 6–8) aligning with MDH-2b of vars. *simplex* (lanes S) and *occidentalis* or three bands (lane 5) aligning with MDH-2b, MHD-2c, and their heterodimer in agamosporous var. *glabella* (lanes G). Thus unlike the previously discussed enzymes, MDH evidence alone does not exclude a combination of the MDH genes of *P. atropurpurea* from the genotypes of the agamosporous tetraploids of the *glabella* complex.

MDH data, however, do strengthen the evidence from other enzymes supporting autopolyploid derivations of the agamosporous tetraploids. The invariant MDH bands of var. *simplex* (Fig. 17, lanes S) correspond to a subset of the bands of var. *occidentalis* seen in Fig. 17, lanes 4, 5, viz. MDH-1c, MDH-1d, and MDH-2b. Similarly, the MDH bands of agamosporous var. *glabella* (Fig. 20, lanes G) correspond to those of sexual var. *glabella* seen in Fig. 20, lanes M, viz. MDH-1c, MDH-2b, and MDH-2c. MDH-1d of var. *simplex* (Fig. 17, lanes S) is coded by an allele that is expressed in var. *occidentalis* (Fig. 17, lane 5) but that has not been found in hundreds of analyzed sporophytes of sexual var. *glabella*. Similarly, MDH-2c in agamosporous var. *glabella* (Fig. 20, lanes G) is coded by an allele expressed in sexual var. *glabella* (Fig. 17, lanes M; Fig. 20, lanes 2, 7, 8) but not found in hundreds of analyzed sporophytes of var. *occidentalis*.

Discussion

Competitive hypotheses concerning the origins of agamosporous taxa in the *P. glabella* complex can be tested by analyzing the taxon-specific electrophoretic enzyme phenotypes of the derivative and potentially progenitor taxa. This study tests hypothesized allopolyploid derivations in which *P. atropurpurea* is one of the progenitor taxa and autopolyploid derivations from the respective sexual taxa in the complex. Present hypotheses of allopolyploidy propose that either (1) *P. atropurpurea* crossed with sexual *P. glabella* var. *occidentalis* giving rise to both var. *simplex* and the agamosporous race of var. *glabella* or (2) *P.*

atropurpurea crossed with *P. glabella* var. *occidentalis* giving rise to var. *simplex* and with the sexual race of var. *glabella* giving rise to the agamosporous race of var. *glabella*. Both allopolyploid hypotheses involve a triploid sperm from agamosporous *P. atropurpurea* and a haploid egg from one of the sexual taxa in *P. glabella*, and in both cases the offspring should be agamosporous tetraploids, as var. *simplex* and the agamosporous race of var. *glabella* are. However, because *P. atropurpurea* would contribute three genome doses via its triploid sperm versus a single genome dose via the haploid egg of the female parent, allopolyploidy also requires the enzyme banding patterns of *P. atropurpurea* to be strongly expressed in the tetraploid offspring. As detailed above and summarized below, the electrophoretic results obtained clearly preclude the involvement of *P. atropurpurea* in the origins of the tetraploids.

At PGM-1, the apparently invariant band in *P. atropurpurea* is not expressed at all in var. *simplex* and is not expressed in var. *glabella* at the intensity expected if this triploid PGM-1 genotype were a constituent of the tetraploid genome of var. *glabella*. Although the tetraploid varieties differ from each other and from *P. atropurpurea* in their PGM-2 banding patterns, the patterns themselves do not preclude the involvement of the *P. atropurpurea* PGM-2 genotype in the genomes of vars. *simplex* and *glabella*. This is because the single strong PGM-2 band of *P. atropurpurea* aligns with a comparably strong band in the agamosporous tetraploids. All PGM bands of var. *simplex* are found in var. *occidentalis* and the only observed source for the slower PGM-2 band of var. *simplex* is var. *occidentalis*. All PGM bands of agamosporous var. *glabella* are found in sexual var. *glabella* except for the orphaned anodal PGM-2 band, and the only observed source for the weak cathodal PGM-1 band of agamosporous var. *glabella* is sexual var. *glabella*.

At PGI-2, the single band of *P. atropurpurea* is only slightly slower than the comparable band in the tetraploids, but this pattern has been observed in numerous gels using plants from a very broad geographic range. The band from *P. atropurpurea* is not found in the tetraploids and therefore *P. atropurpurea* has not contributed its PGI-2 genotype to them. Because var. *occidentalis* and sexual var. *glabella* both produce the PGI-2 allozyme found in var. *simplex* and in one-banded populations of agamosporous var. *glabella*, PGI itself is not sufficient to determine which sexual entity may have been the progenitor of var. *simplex* and those populations of var. *glabella*. These PGI-2 data are consistent, however, with an origin of var. *simplex* from var. *occidentalis* as suggested by PGM-2 and with an origin of agamosporous var. *glabella* from sexual var. *glabella* as suggested by PGM-1. The three-banded PGI-2 pattern of agamosporous var. *glabella* includes a more anodal allozyme (and heterodimer) for which the only observed source is sexual var. *glabella*.

The TPI-1 allozyme patterns of the three agamosporous taxa each migrate to different positions, and the constituent bands are not aligned from taxon to taxon. As with PGM-1 and PGI-2, the electrophoretic mobility of TPI-1 in *P. atropurpurea* indicates that the triploid TPI-1 genotype of that species is not a constituent of the tetraploid genotypes of the agamosporous varieties. At TPI-2, the relative staining intensities of the bands in these three taxa are the opposite of

what would be expected if the genotype of *P. atropurpurea* comprised three-fourths of the genomes of the tetraploid varieties. The TPI patterns of Figure 13, in which true hybrids are compared to the taxa under discussion, confirm this and reject hypotheses involving triploid *P. atropurpurea* in the derivations of var. *simplex* and agamosporous var. *glabella*. At TPI-1, the slower three-banded pattern common to var. *occidentalis* and sexual var. *glabella* characterizes agamosporous var. *glabella* and is combined with three doses of the faster three-banded pattern of var. *occidentalis* to yield the heterozygous TPI-1 pattern of var. *simplex*. Thus TPI-1 data are consistent with an autoploid derivation of agamosporous var. *simplex* from sexual var. *occidentalis* and with an autoploid origin of agamosporous var. *glabella* from sexual var. *glabella* or from sexual var. *occidentalis*. Because TPI-2 patterns are identical in the agamosporous tetraploids and because the requisite coding alleles are found in both sexual taxa, TPI-2 itself is not definitive in establishing progenitor-derivative lineages although it is consistent with interpretations based on other enzymes.

Pellaea atropurpurea cannot contribute to the SkDH patterns of the tetraploid varieties because they lack the anodal band of most *P. atropurpurea* populations. Hybridization involving the more cathodal single-banded SkDH pattern of *P. atropurpurea* (as in Fig. 14, lane 6) would yield a tetraploid in which the cathodal band has three times the intensity of the anodal band, a pattern not observed in vars. *simplex* and *glabella*. Both allozymes of var. *simplex* are observed in var. *occidentalis*, but only the stronger more anodal band of agamosporous var. *glabella* has been observed in sexual var. *glabella*, the faint cathodal band being orphaned or too infrequent for detection in samples available from the sexual populations.

Although genetic interpretations of the AAT patterns in this complex are not presently available, observed patterns of triploid *P. atropurpurea* could not combine with the pattern of any haploid genotype to yield the AAT phenotypes of tetraploid vars. *simplex* and *glabella*. Thus AAT at least provides an additional independent data set inconsistent with allopolyploid hypotheses involving *P. atropurpurea*.

For MDH-2 and MDH-3, various sporophytes of *P. atropurpurea* express the same bands as the agamosporous tetraploids. For MDH-1, *P. atropurpurea* expresses the same band as agamosporous var. *glabella* and the major band expressed by var. *simplex*. Thus MDH data do not exclude *P. atropurpurea* from the ancestry of the agamosporous tetraploids as other enzyme data do. However, MDH data are consistent with derivations of the agamsporous tetraploids from the sexual diploids alone. Moreover, based on these extensive survey data of the four taxa within the *P. glabella* complex, the allele coding the cathodal MDH-1 allozyme of var. *simplex* (MDH-1d) could only have come from sexual var. *occidentalis* and the allele coding the cathodal MDH-2 allozyme of agamosporous var. *glabella* (MDH-2c) could only have come from sexual var. *glabella*. Even without the corroborating data from PGI, PGM, and TPI above, these MDH data suggest that agamosporous tetraploid var. *simplex* is an autopolyploid derivative of sexual diploid var. *occidentalis* and that

FIG. 21. Sporophytes representing the *P. glabella* complex and *P. atropurpurea*. Acronyms identifying populational sources are as in Table 1. Millimeter bar represents reduction by 0.25.

agamosporous tetraploid var. *glabella* is an autopolyploid derivative of sexual diploid var. *glabella*.

Thus the agamosporous tetraploids do not express the electrophoretic phenotypes expected for at least six isozymes (PGM-1, PGI-2, TPI-1, TPI-2, SKDH, AAT) if *P. atropurpurea* were one of their progenitors. Therefore *P. atropurpurea* could not have crossed with sexual var. *occidentalis* to give rise to var. *simplex* to the west and var. *glabella* to the east as proposed in one of Tyron's (1957) hypotheses and as accepted for var. *simplex* (as *P. suksdorfiana*) by Lellinger (1985). Nor are the observed electrophoretic patterns those expected if *P. atropurpurea* sired the agamosporous taxa through respective hybridizations with the two sexual taxa now known in the *P. glabella* complex. Furthermore, as seen in Fig. 21, the morphologies of agamosporous tetraploid vars. *glabella* (G14) and *simplex* (S2) are not what should be expected if the triploid genome of *P. atropurpurea* (A3) were combined with the haploid genome of var. *occidentalis* (04, 06) or sexual var. *glabella* (M2) to produce them. The hypotheses involving *P. atropurpurea* in the derivation of the tetraploid agamosporous varieties of *P. glabella* are therefore rejected.

An alternative hypothesis for the derivations of the agamosporous taxa in the *glabella* complex is that they arose through hybridizations between sexual var. *glabella* and var. *occidentalis*. Under this hypothesis, the electrophoretic differences observed between the agamosporous taxa would be attributable to

TABLE 2. Occurrences In the Sexual Taxa of the Allozyme Bands That Characterize the Agamosporous Taxa of the *Pellaea glabella* Complex.

	PGM-1	PGM-2	PGI-2	TPI-1	TPI-2	SKDH	MDH-1	MDH-2
simplex								
anodal band[1]	both[2]	both	both	occi[3]	both	both	both	both
cathodal band		occi		both	both	occi	occi	
glabella								
anodal band	both	orbo[4]	glab[5]	both	both	both	both	both
cathodal band	glab	both	both		both	orgl[6]		glab

[1]Or the only band for this isozyme when no cathodal allozyme was observed.
[2]Indicates that the allele coding this band is found in both sexual taxa.
[3]Indicates that the allele coding this band is found only in var. *occidentalis*.
[4]Indicates that the allele coding this band is orphaned, not found in either sexual taxon.
[5]Indicates that the allele coding this band is found only in sexual var. *glabella*.
[6]The allele coding this band is found in both agamosporous taxa and in var. *occidentalis* but is orphaned from sexual var. *glabella*.

independent origins of these taxa from sexual individuals of differing genotypes. The electrophoretic data presented here cannot directly reject this hypothesis. For each of the isozymes summarized in Table 2, the genes coding at least one of the bands of the agamosporous tetraploids could be derived from either sexual variety. Thus var. *simplex* could be a hybrid of the two sexual taxa as long as var. *occidentalis* contributed the allele coding the cathodal allozyme of PGM-2, SKDH, and MDH-1 and the anodal allozyme of TPI-1. Similarly, agamosporous var. *glabella* could be a hybrid of the two sexual taxa as long as sexual var. *glabella* contributed the allele coding the cathodal allozyme of PGM-1 and MDH-3 and the anodal allozyme of PGI-1.

Two lines of evidence, however, argue against this hypothesis. One is the gross morphology of the sporophytes of these taxa. The agamosporous tetraploids simply do not look like crosses between the sexual taxa. Instead, as seen in Fig. 22, tetraploid var. *simplex* (S2) looks like a robust form of diploid var. *occidentalis* (04) and tetraploid agamosporous var. *glabella* (G14) looks like a robust form of diploid sexual var. *glabella* (M2). Wagner et al. (1965), for example, were unable to find morphological distinctions between the two reproductive types of var. *glabella* except in the number of spores per sporangium.

The second line of evidence concerns which sexual taxon is the source of the allozymes unique to the respective agamosporous taxa. In all cases in which var. *simplex* and agamosporous var. *glabella* are distinguished from each other by an alloyzme that they do not share and that is not found in both sexual progenitors (Table 2), the distinguishing allozyme of var. *simplex* always comes from var. *occidentalis* and the distinguishing allozyme of agamosporous var. *glabella* always comes from sexual var. *glabella*. If the agamosporous taxa were hybrids of the two sexual taxa, one should expect a more random distribution of the distinctive allozymes—some of the allozymes unique to sexual var. *occidentalis*

FIG. 22. Sporophytes illustrating the morphology of taxa in the *P. glabella* complex. Acronyms identifying populational sources are as in Table 1. Millimeter bar represents reduction by 0.31.

should occur in agamosporous var. *glabella* and some of the allozymes unique to sexual var. *glabella* should occur in agamosporous var. *simplex*. This is not observed. On the contrary, the morphological and electrophoretic data are consistent with the hypothesis that var. *simplex* is an autopolyploid derivative of var. *occidentalis* and agamosporous var. *glabella* is an autopolyploid derivative of sexual var. *glabella*. This study accepts the latter hypothesis and invokes the mechanism of unreduced spores (Gastony, 1986) to account for the tetraploidy of the agamosporous derivatives.

TAXONOMIC CONCLUSIONS

The taxonomic interrelationships of *P. atropurpurea* and the three *P. glabella* taxa known before 1965 have long been problematic, as indicated by the synonymies in Tryon's revision (1957). Morphological, ploidal, and ecological differences justifying taxonomic distinction between these taxa have been summarized and discussed by several authors (Rydberg, 1900; Butters, 1917, 1921a, 1921b; Tryon, 1957; Tryon & Britton, 1958; Rigby & Britton, 1970; Brunton, 1979; Lellinger, 1985). Enzyme electrophoretic data presented above exclude *P. atropurpurea* from the phylogeny of the *P. glabella* taxa and provide new insights into the progenitor-derivative relationships of the four taxa now known in the complex. These phyletic relationships should be reflected in a revised taxonomy of this group. The evolutionary lineage of var. *occidentalis* with its autopolyploid agamosporous derivative var. *simplex* shows substantial morphological discontinuity with the lineage of sexual var. *glabella* and its

autopolyploid agamosporous derivative (Figs. 21, 22), and this correlates with the electrophoretic discontinuity detailed above. These two lineages should therefore be recognized as separate species. At specific rank, the two sexual progenitors must be known as *Pellaea glabella* and *P. occidentalis*.

In addition to their ploidy differences, the sexual and agamosporous taxa of *P. glabella* in this narrow revised sense are reliably distinguished at the morphological level only by the number of spores per sporangium and the sizes of cells influenced by ploidy. Electrophoretically detected genotypes of the agamosporous tetraploid are a subset of the genetic variants found in the progenitor sexual diploid. In living condition, the sexuals tend to have a more bluish tint than the more greenish tinted tetraploids, and the leaf segments of the tetraploids tend to be broader and more triangularly shaped than those of the sexual diploids. However, in common greenhouse culture none of these distinctions is consistently reliable. Moreover, both the diploids and the tetraploids survive equally well under common greenhouse cultural conditions, reflecting their similar physiological-ecological amplitude. Thus, the agamosporous taxon exhibits neither the substantial morphological discontinuity nor the genetic discontinuity from its sexual progenitor that would be implied by separating them at the species level. The electrophoretic distinction of the true-breeding agamosporous tetraploid derives simply from gene dosage effects associated with autopolyploidy and banding pattern fixation caused by lack of genetically significant segregation in agamosporous sporogenesis. The distinction between these taxa therefore seems best recognized at the level of varieties.

In the case of *P. occidentalis* as well, the agamosporous autotetraploid is fixed for a subset of the sexual's alleles, much as any one population of the sexual diploid might encompass only part of the combined variation of all the diploid populations. As in the preceding case, this degree of genetic continuity between sexual progenitor and agamosporous derivative argues against distinction between these taxa at the rank of species. In this case, however, there is slight morphologial discontinuity (perhaps partially attributable to a gigas effect in the tetraploid), so that the diploids and tetraploids have long been distinguished taxonomically at the rank of variety (Butters, 1917; Tryon, 1957) or even species (Butters, 1921a, 1921b; Brunton, 1979; Lellinger, 1985). The morphological discontinuity described by the cited authors and the physiological differences indicated by the tetraploid's prolonged survival under greenhouse cultural conditions soon lethal to the diploids have an underlying, although unquantified, genetic basis. These differences indicate a greater degree of genetic distinction between the infra-specific taxa of *P. occidentalis* than between those of *P. glabella*. This greater degree of divergence within *P. occidentalis* should be reflected in the taxonomic rank assigned to its infraspecific taxa. Thus in contrast to varietal distinction within *P. glabella*, the nearly disjunctly distributed infraspecific taxa of *P. occidentalis* are distinguished at the slightly higher rank of subspecies.

The foregoing considerations are reflected in the following revision of taxonomic relationships within the *P. glabella* complex sensu Tryon (1957) and Wagner et al. (1965).

1. *Pellaea glabella* Mett. ex Kuhn, Linnaea 36:87. 1869.

1a. *Pellaea glabella* var. *glabella* (Fig. 1, GLAa; Fig. 22,G14).

Although I have not examined the type (Missouri, Kimmswick near St. Louis, presumably *B*), its provenance and the more common occurrence of the tetraploid promote the assumption that it represents the 32-spored agamosporous tetraploid. See Tryon (1957, p. 141) for full synonymy.

1b. **Pellaea glabella** var. **missouriensis** Gastony, var. nov. (Fig. 1, GLAs; Fig. 22, M2).—TYPE: Missouri, Jefferson Co., river bluffs 10 miles W of DeSoto, near jct. of road H and Big River, *Gastony 83-34-47* (IND; isotypes GH, MICH, MO); paratype (from same locality): *Farrar s.n.* (MICH).

A varietate *glabella* varietas haec distinguitur sporarum numero hic 64 per sporangium illic 32, chromosomatum numero hic 29 II illic 58 II.

The varietal epithet for this 64-spored, sexually reproducing, diploid variety is based on its discovery by Donald Farrar in Missouri (Wagner et al., 1965) and on the restriction of its present known range to the small area of Missouri (Fig. 1, GLAs) encompassing the localities cited in Table 1 and in Wagner et al. (1965). Occasional pentaploid hybrids between the two varieties of *P. glabella* were discovered in populations from Missouri during this study. These are 32-spored and their electrophoretic phenotypes combine those of the parental varieties.

2. *Pellaea occidentalis* (E. E. Nelson)Rydb., Mem. New York Bot. Gard. 1:466. 1900

2a. *Pellaea occidentalis* subsp. *occidentalis* (Fig. 1, OCC; Fig. 22, 04 and 06).

This is the taxon known as *Pellaea glabella* var. *occidentalis* (E. E. Nelson) Butters in Tryon (1957, p. 139) where full synonymy can be found.

2b. **Pellaea occidentalis** subsp. **simplex** (Butters) Gastony, comb. et stat. nov. (Fig. 1 SIM; Fig. 22, S2).—*Pellaea glabella var. simplex* Butters, Amer. Fern J. 7:84. 1917.

This is the taxon known as *Pallaea glabella* var. *simplex* in Tryon (1957, p. 142) where full synonymy can be found.

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LITERATURE CITED

ALTSCHULER, M. I. and D. SCHWARTZ. 1983. Minor electrophoretic forms of maize alcohol dehydrogenase: their *in vitro* production by ß-mercaptoethanol. Maydica 28:401–410.

BRUNTON, D. F. 1979. Taxonomy, distribution, and ecology of the cliff-brake ferns (*Pellaea*: Polypodiaceae) in Alberta. Canad. Field-Naturalist 93:288–295.

——— and J. D. LAFONTAINE. 1974. The distribution of *Pellaea* in Quebec and eastern Ontario. Naturaliste Canad. 10:937–939.

BRYAN, F. and D. E. SOLTIS. 1987. Electrophoretic evidence for allopolyploidy in the fern *Polypodium virginianum*. Syst. Bot. 12:553–561.

BUTTERS, F. K. 1917. *Pellaea atropurpurea* (L.) Link and *Pellaea glabella* Mett. ex Kuhn. Amer. Fern J. 7:77–87.

———. 1921a. A new western species of *Pellaea*. Amer. Fern J. 11:39–40.

———. 1921b. Taxonomic and geographic studies in North American ferns. III. *Pellaea glabella* and its western segregates. Amer. Fern J. 11:75–82.

GASTONY, G. J. 1986. Electrophoretic evidence for the origin of fern species by unreduced spores. Amer. J. Bot. 73:1563–1569.

——— and D. C. DARROW. 1983. Chloroplastic and cytosolic isozymes of the homosporous fern *Athyrium filix-femina*. Amer. J. Bot. 70:1409–1415.

——— and L. D. GOTTLIEB. 1982. Evidence for genetic heterozygosity in a homosporous fern. Amer. J. Bot. 69:634–637.

——— and ———. 1985. Genetic variation in the homosporous fern *Pellaea andromedifolia*. Amer. J. Bot. 72:257–267.

GOTTLIEB, L. D. 1981. Electrophoretic evidence and plant populations. Progr. Phytochem. 7:1–46.

———. 1982. Conservation and duplication of isozymes in plants. Science 216:373–380.

HAUFLER, C. H. 1985. Enzyme variability and modes of evolution in *Bommeria* (Pteridaceae). Syst. Bot. 10:92–104.

———, M. D. WINDHAM, D. M. BRITTON, and S. J. ROBINSON. 1985. Triploidy and its evolutionary significance in *Cystopteris protrusa*. Canad. J. Bot. 63:1855–1863.

——— and D. E. SOLTIS. 1986. Genetic evidence suggests that homosporous ferns with high chromosome numbers are diploid. Proc. Natl. Acad. U.S.A. 83:4389–4393.

LELLINGER, D. B. 1985. *A field manual of the ferns & fern allies of the United States & Canada*. Washington: Smithsonian Institution Press.

LÖVE, Á. and D. LÖVE. 1975. *Plant Chromosomes*. Vaduz: J. Cramer.

PICHERSKY, E. and L. D. GOTTLIEB. Evidence for duplication of the structural genes coding plastid and cytosolic isozymes of triose phosphate isomerase in diploid species of *Clarkia*. Genetics 105:421–436.

RIGBY, S. J. 1968. An investigation of *Pellaea glabella* Mett. ex Kuhn and *Pellaea atropurpurea* (L.) Link and their relationships. Master's Thesis University of Guelph, Guelph, Ontario, Canada.

——— and D. M. BRITTON. 1970. The distribution of *Pellaea* in Canada. Canad. Field-Naturalist 84:137–144.

ROOSE, M. L. and L. D. GOTTLIEB. 1976. Genetic and biochemical consequences of polyploidy in *Tragopogon*. Evolution 30:818–830.

RYDBERG, P. A. 1900. Catalogue of the flora of Montana and the Yellowstone national park. Mem. New York Bot. Gard. 1:1–492.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, and J. B. GENTRY. 1971. IV. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Studies in genetics VI. Univ. Texas Publ. 7103:49–90.

SOLTIS, D. E. 1986. Genetic evidence for diploidy in *Equisetum*. Amer. J. Bot. 73:908–913.

———, C. H. HAUFLER, D. C. DARROW, and G. J. GASTONY. 1983. Starch gel electrophoresis of ferns: A compilation of grinding buffers, gel and electrode buffers, and staining schedules. Amer. Fern J. 73:9–27.

——— and P. S. SOLTIS. 1986. Electrophoretic evidence for inbreeding in the fern *Botrychium virginianum* (Ophioglossaceae). Amer. J. Bot. 73:588–592.

TRYON, A. F. 1957. A revision of the fern genus *Pellaea* section *Pellaea*. Ann. Missouri Bot. Gard. 44:125–193.

———. 1972. Spores, chromosomes, and relations of the fern *Pellaea atropurpurea*. Rhodora 74:220–241.

——— and D. M. BRITTON. 1958. Cytotaxonomic studies of the fern genus *Pellaea*. Evolution 12:137–145.

WAGNER, W. H., D. R. FARRAR, and K. L. CHEN. 1965. A new sexual form of *Pellaea glabella* from Missouri. Amer. Fern J. 55:171–178.

WALKER, T. G. 1962. Cytology and evolution in the fern genus *Pteris* L. Evolution 16:27–43.

———. 1979. The cytogenetics of ferns. Pp. 87–132 in *The experimental biology of ferns*, ed. A. F. Dyer. New York: Academic Press.

WEEDEN, N. F. 1983. Plastid isozymes. Pp. 139–156 in *Isozymes in plant genetics and breeding*, part A, eds. S. D. Tanskley and T. J. Orton. Amsterdam: Elsevier Science Publishers B.V.

WERTH, C. R., S. I. GUTTMAN, and W. H. ESHBAUGH. 1985. Electrophoretic evidence of reticulate evolution in the Appalachian *Asplenium* complex. Syst. Bot. 10:184–192.

APPENDIX: Interpreting the Non-Segregating Three-banded TPI-1 Pattern in Ferns

As indicated in the text (p. 52), one zone of TPI activity in ferns is commonly expressed as a fixed, asymmetrically stained, three-banded pattern. This pattern usually occurs as the more anodally migrating zone of activity (TPI-1) and has been explained as resulting from a single gene duplication or from post-translational modification of some of the coded protein.

The three-banded TPI-1 pattern is explained by the gene duplication hypothesis in the following way. The original *tpi-1* gene has undergone a (possibly tandem) duplication and the duplication has subsequently mutated. Thus the protein coded by the original form of the gene and the protein coded by the modified duplicate gene migrate to slightly different gel positions during electrophoresis, and the expected interlocus heterodimeric protein migrates to a position midway between them. One of these two coded enzymatic proteins is considerably less active than the other, so that the most anodal of the three bands is faintly stained, the most cathodal is normally stained, and the intensity of the central interlocus heterodimeric band is roughly equal to that of the normally stained cathodal homodimer.

Because the original gene and its duplication are independent loci, there is no reason to expect the duplicate gene to develop an allelic variant whenever the original gene does so. If an allelic variant of the original gene does arise, we should expect the allozyme coded by the variant allele to migrate to its own gel position and to form both the usual intralocus heterodimer and an interlocus heterodimer midway between itself and the protein coded by the duplicate gene. This, however, is not what we observe in ferns. Instead, when the locus encoding TPI-1 is heterozygous, it codes two distinct three-banded patterns plus new heterodimeric bands (theoretically totaling ten bands), but heterozygotes usually appear as a four-banded to seven-banded pattern depending on the number of overlapping or nearly overlapping bands and on the faintness of the anodal homodimers. This is illustrated in Fig. 7, where lanes 5 and 7 show two variant three-banded TPI-1 patterns from sporophytes of sexual diploid *P. glabella* var. *occidentalis* and lanes 6 and 10 show the pattern in another sporophyte in which at least seven bands are distinguishable at TPI-1. Application of the gametophytic segregation technique of Gastony and Gottlieb (1982) shows that this multi-banded, heterozygous, sporophytic pattern segregates into faster (lanes 3, 8) and slower (lanes 4, 9) three-banded patterns in individual gametophytes derived from the sporophyte in lanes 7 and 10. Similar segregation of TPI-1 patterns have been observed in sexually reproducing var. *glabella* (Fig. 8, lanes 10–12) and in *Cystopteris protrusa* (Haufler et al., 1985; Haufler & Soltis, 1986), indicating that the three-banded patterns are allelic to each other.

The hypothesis of gene duplication provides an improbable explanation of this situation. This is because when an allelic variant of the original gene occurs, that variant allele is also expressed as a three-banded pattern, as shown in Fig. 7. If each three-banded pattern were coded by a gene and its duplication, then whenever an allelic variant of the original gene arose, the duplicate gene would also have to generate a new allele, since each observed allelic segregant occurs as a three-banded pattern. It is simply improbable that each allelic variant of the original gene would always be associated with a new allelic variant of the duplicate gene in var. *occidentalis* and in sexual var. *glabella*. It is even more improbable that this should also be the case in the unrelated fern species *Cystopteris protrusa* where the allelic variants also occur as three-banded patterns (Haufler et al., 1985; Haufler & Soltis, 1986). Analogous three-banded allelic variants may also underlie the complex cathodal TPI patterns of diploid *Polypodium virginianum* (Bryan & Soltis, 1987). It is unlikely that independent loci would act in this way in all known cases of this kind in the ferns.

The alternative explanation for the three-banded TPI-1 pattern is that a gene which may be homozygous or heterozygous codes a protein naturally susceptible to a charge modification during protein synthesis or post-translationally. When the gene is homozygous, the coded monomeric

protein and a charge-modified form of some of it are produced. These monomers combine randomly to form the dimeric quaternary structure of the functional enzyme. The most anodal band of the three-banded pattern consists of less active, homodimeric, protein; the most cathodal band of the triplet consists of normally active, homodimeric protein; and the central band of the triplet represents hetrodomeric protein. Generally with dimeric enzymes, when two different monomeric forms of a protein occur in the same subcellular compartment, they combine randomly to form the dimeric functional form of the enzyme. This usually results in a 1:2:1 ratio of homodimer:heterodimer:homodimer staining intensities. In the case of TPI-1 in the *P. glabella* complex and *Cystopteris protrusa*, because one of the monomers is less active than the other, their random association results in a ratio of activity that is not 1:2:1 but rather approximately 1:1:less-than-1 when read from the cathodal end. In diploid sporophytes that are heterozygous at *tpi-1*, two allelically coded monomers and two charge-modified forms of those monomers would be produced, and heterodimeric functional enzymes would be formed by all dimeric combinations of the four monomers. This would yield 10 enzyme bands if none were overlapping. The migration distances and staining intensities of the novel heterodimeric bands are predictable from the positions and degrees of activity of the component monomers and from the expected relative dosages of the heterodimers. In the case of var. *occidentalis*, the predictions agree with observations, as in Fig. 7 lane 6. Thus the three-banded TPI-1 patterns in ferns are herein accepted as specified by a single *tpi-1* locus, a portion of whose protein product is regularly affected by post-translational charge modification.

This interpretation of these fixed three-banded TPI patterns in ferns is supported by a parallel situation with dimeric alcohol dehydrogenase in maize (Altschuler & Schwartz, 1983). In maize, *in vivo* anodal minor ADH bands associated with prolonged storage of dried seed could also be produced *in vitro* by treating enzyme extracts with ß-mercaptoethanol. Experiments based on this observation lead Altschuler & Schwartz (1983) to conclude that the anodal minor ADH bands are of post-translational origin. Although some agent (or combination of agents) other than ß-mercaptoethanol may cause post-translational modification of this TPI isozyme in ferns, it is noteworthy that ß-mercaptoethanol (as 2-mercaptoethanol) is a component of the three grinding buffers most commonly used in electrophoresis of ferns (Soltis et al., 1983). In the *P. glabella* complex, however, three-banded forms of TPI-1 persist even if 2-mercaptoethanol is eliminated from the grinding buffer. In maize ADH, the electrophoretic mobility of anodal minor bands was always correlated with that of the major band, and mutations that altered the electrophoretic mobility of the major band also altered the mobility of the minor bands to the same degree. This is precisely what is observed with TPI in the ferns.

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Marsilea scalaripes, A New Member of *Marsilea* section *Clemys* from the Asian Tropics

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A specimen of *Marsilea* collected by E. J. H. Corner in Kedah, Malaysia, in 1941 has been the basis for reports of the primarily Neotropical *M. polycarpa* Hook. & Grev. from the Asian tropics (Holttum, 1954; Launert, 1968). Both of these authors observed, however, that this specimen probably represented a distinct species. My revision of the New World species of *Marsilea* (Johnson, 1986) afforded me an opportunity to study abundant material of *Marsilea polycarpa* and then to compare it to a fragment of *Corner S.F.N. 38109* in the herbarium of the British Museum. Even from this small sample it was apparent that the specimen was of a species distinct from *M. polycarpa*, and a loan of the full sheet of the collection from the herbarium of the Singapore Botanic Gardens (SING) confirmed this. I provide here a full description of this new species, and discuss its relationship to the other members of the small but well-defined sect. *Clemys* of *Marsilea*.

Marsilea scalaripes D. M. Johnson, sp. nov. (Fig. 1A–E)—TYPE: Malaysia, Kedah, 1941, *Corner S.F.N. 38109* (SING!; fragment BM!).

A *Marsilea polycarpa* Hook. & Grev. sporocarpiis ovoideis 3.1–4.5 mm longis, sporocarpio infimo 2.1–4.7 cm supra basim petioli portato, a *M. crotophora* D. M. Johnson sporocarpiis aspectu frontali tereti, 2.0–2.5 mm latis, ab ambobus pedunculo 3.1–7.8 mm longis recedit.

Rhizome long-creeping, 1.0–1.5 mm thick, pale brown to stramineous, densely pubescent at apex, soon glabrate proximally, with internodes 1.2–5.0 cm long; nodal shoots suppressed, budlike; roots at nodes and 1–2 on internodes. Land leaves with canaliculate petioles 13.7–15.0 cm long, 0.7–1.3 mm thick, curved to straight, glabrescent; leaflets 16–17 mm long, 13.5–14.5 mm wide, sparsely pubescent adaxially, glabrous abaxially, lateral margins straight or slightly concave, terminal margin entire. Floating leaves with flexuous canaliculate petioles 9.8–11.7 mm long, 0.8–1.2 mm thick, glabrous; leaflets 14–16 mm long, 12–14 mm wide, glabrous, with hydropoten uniformly distributed abaxially. Fertile leaves bearing 4–9 sporocarps on unbranched straight or slightly curving, weakly to strongly ascending peduncles 3.1–7.8 mm long, 0.5–0.6 mm thick, thinly pubescent to glabrate, in a row beginning 2.1–4.7 cm above the petiole base and extending distally for 6–19 mm, the bases of the peduncles expanded and thus almost confluent at base. Sporocarps 3.1–4.5 mm long, 2.0–2.5 mm wide, and 2.0 mm thick, ovoid, terete in cross-section (i.e., frontal aspect), dark brown, thinly covered with matted hairs; raphe and teeth

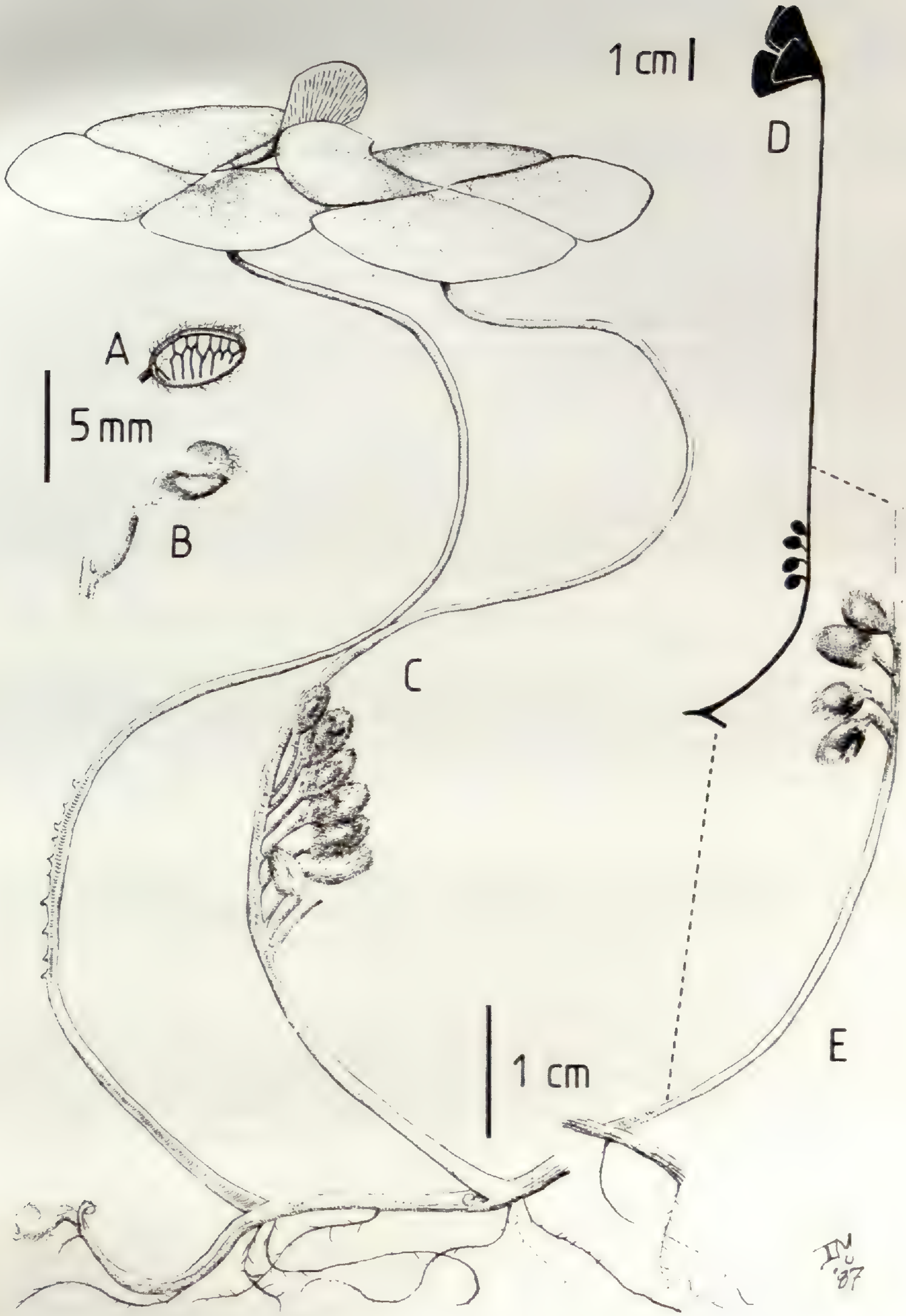

FIG. 1. *Marsilea scalaripes* D. M. Johnson. A, sporocarp in longitudinal section, showing venation in one wall. B, sporocarp, enlarged. C, habit, floating leaves (leaflets reconstructed). D, habit, land leaf. E, sporocarp-bearing portion of land leaf, enlarged. All based on Corner S.F.N. 38109 (SING).

absent; sporocarp veins ca. 15–16, connected by a zigzag lateral vein 1/3 distance from the midrib. Sori 11, attached to a sorophore that tapers to a blunt tip, with 1–3 megasporangia and an undetermined number of microsporangia per sorus. Megaspores 560–650 μm long and 480–500 μm wide, with a papilla 50–90 μm long. Microspores ca. 40 per sporangium, 35–50 μm in diameter [probably immature].

The specific epithet is from Latin signifying "ladder-foot," alluding to the series of more or less parallel runglike sporocarp peduncles of the new species.

Marsilea scalaripes is probably closest to *M. polycarpa* but differs in the high position of its sporocarps, longer peduncles, and longer sporocarps. The high position of the sporocarps on the petiole is like that of *M. crotophora*, a Neotropical species with the lowest sporocarp attached 1.1–7.5 cm above the petiole base; the sporocarps of that species are, however, pear-shaped, ovate in cross-section, and borne on strongly recurved peduncles only 1.7–2.7 mm long.

Sporocarp length and shape are more reliable as taxonomic characters than is peduncle length. The peduncles on floating leaves of *Corner S.F.N. 38109* were 4.7–7.8 mm long ($\bar{x} = 5.70 \pm 0.99$, $n = 10$), while those of the land leaves were only 3.1–5.2 mm long ($\bar{x} = 4.08 \pm 0.62$, $n = 8$). Sporocarp length, in contrast, was 3.1–4.5 mm on the floating leaves ($\bar{x} = 3.85 \pm 0.49$, $n = 10$), and 3.1–4.0 mm on the land leaves ($\bar{x} = 3.50 \pm 0.26$, $n = 8$). This further supports the point made elsewhere (Bhardwaja, 1967; Johnson, 1986) that peduncle length is environmentally plastic.

Marsilea scalaripes, although only known from a herbarium specimen, appears to be, like other members of sect. *Clemys*, a strictly aquatic species. The type specimen has samples of floating leaves and of land leaves, both of which are fertile. Only the Neotropical *M. deflexa* A. Braun (Johnson, 1986) and the African *M. berhautii* Tardieu (Kornaś, 1983) are known to produce sporocarps abundantly in water. Another character correlated with an aquatic life cycle in *Marsilea* is the absence of simple perforation plates in root metaxylem elements. *Marsilea scalaripes*, along with *M. deflexa* and *M. crotophora* of sect. *Clemys*, lacks these plates; all other species of *Marsilea* investigated to date have them (White, 1961; Mehra & Soni, 1971; Bhardwaja & Baijal, 1977; Johnson, 1986).

The members of *Marsilea* sect. *Clemys* and their distributions now stand as follows: 1) *M. deflexa*, Mexico to South America; 2) *M. berhautii*, western tropical Africa, 3) *M. crotophora*, Mexico, Central America, and western South America; 4) *M. scalaripes*, Malay Peninsula; and 5) *M. polycarpa*, Mexico to northern South America, Greater Antilles, and the Society Islands of the South Pacific.

Acknowledgments

I thank the curators of the herbaria of the British Museum (Natural History) and Singapore Botanic Gardens for making specimens available for my study, and W. R. Anderson of the University of Michigan Herbarium for requesting and transferring specimens sent on loan. My visit to English herbaria was made possible by a Rackham Dissertation Grant from the University of Michigan. I thank N. A. Murray and R. E. Holttum for comments on the manuscript.

Literature Cited

Bhardwaja, T. N. 1967. Pedicel attachment in *Marsilea diffusa* var. *approximata* in relation to habitat factor. Trop. Ecol. 8:17–21.

———, and J. Baijal. 1977. Vessels in rhizome of *Marsilea*. Phytomorphology 27:206–208.

Holttum, R. E. 1954. *A revised flora of Malaya*. Vol. 2, *Ferns of Malaya*. Singapore: Government Printing Office.

Johnson, D. M. 1986. Systematics of the New World species of *Marsilea* (Marsileaceae). Syst. Bot. Monogr. 11:1–87.

Kornaś, J. 1983. Pteridophyta collected in northern Nigeria and northern Cameroon. Acta Soc. Bot. Poloniae 52:321–335.

Launert, E. 1968. A monographic survey of the genus *Marsilea* Linnaeus, I: the species of Africa and Madagascar. Senckenberg. Biol. 49:273–315.

Mehra, P. N., and S. L. Soni. 1971. Morphology of the tracheary elements in *Marsilea* and *Pilularia*. Phytomorphology 21:68–70.

White, R. A. 1961. Vessels in the roots of *Marsilea*. Science 133:1073–1074.

Shorter Notes

Rediscovery of Gymnocarpium dryopteris in Arizona—During the summer of 1986, biologists for the Coconino National Forest conducted riparian surveys in the East Clear Creek drainage of the Colorado Plateau. A high priority was placed on the development of an accurate plant species list since none was available for the area. Many new distribution records were recorded. Identification was accomplished with the help of taxonomists from the Deaver Herbarium at Northern Arizona University (ASC), Flagstaff, Arizona.

A plant collection of particular interest was the Oak Fern, *Gymnocarpium Dryopteris* (L.) Newm., which was collected in Dane Canyon, along a perennial stream, approximately 19 kilometers (12 miles) SSE of the Blue Ridge Ranger Station in Coconino County. Two plants were discovered, and at the time of collection both plants were fertile. The plants were on a sandstone ledge adjacent to the creek bottom. The exposure was north-facing in a steep, narrow canyon. The associated vegetation was riparian shrub with a coniferous overstory. A portion of the plant (*Boucher 500*, ASC 48519) was collected on 17 August 1987.

The new locality for this widespread, primarily boreal species is only the second recorded station for Arizona. The first collection was made from Bonito Creek, in the White Mountains of Apache County, Arizona 23 July 1912, by L. N. Goodding. *Goodding 1222* (ARIZ 6964, 6965) and *Goodding 1252a* (ARIZ 6968), are housed at the University of Arizona Herbarium, Tucson, Arizona. Recent attempts to relocate this original population have proven unsuccessful. At present, the only living plants known from Arizona are the two plants located in Dane Canyon.—Paul F. Boucher, USDA Forest Service, Coconino National Forest, 2323 East Greenlaw Lane, Flagstaff, Arizona 86004.

The Status of *Asplenium viride* in Oregon—*Asplenium viride* Huds. was discovered in Oregon in 1908 by William C. Cusick (Mason, G., *Guide to the Plants of the Wallowa Mountains of Northeastern Oregon*. Museum of Natural History, Univ. of Oregon, Eugene, 2nd ed., 1980). The label data on Cusick's sheet (*Cusick s.n.*, ORE) seem to pinpoint the locality: "Granitic cliffs, source of the Imnaha River, 9000 feet alt." A pencilled annotation on the original label asks: "limestone cliffs?" Since this was the only historical record for green spleenwort in Oregon, I was interested in relocating the population, which had not been seen since 1908 and was believed to be "apparently extirpated" from Oregon (Kagan, J, S. Yamamoto & C. Levesque, *Rare, Threatened & Endangered Plants and Animals of Oregon*. Oregon Natural Heritage Data Base, Portland, 1987.)

The source of the Imnaha River is in the remote high country of the Eagle Cap Wilderness in the Wallowa Mountains of northeastern Oregon. Four main forks converge to form the Imnaha, which flows east through the Wallowa-Whitman National Forest. The headwaters encompass roughly 15 square kilometers of alpine and sub-alpine terrain. At least six peaks and many ridges rise above 2740 meters (9000 feet) in the watershed. The bedrock is mostly pale grey or white limestone, but some outcrops of a white granite (granodiorite) are also exposed.

In the summer of 1987 I examined the various headwaters of the Imnaha. I found a small population of *Asplenium viride* in the cirque at the head of the Middle Fork of the Imnaha River (T 5 S, R 45 E, S 9 NW 1/4 NW 1/4, Wallowa County). The site is at 45° 8' 57" N, 117° 13' 23" W, and is 1.5 km SSE of Sentinel Peak. The ferns were on a large, white Triassic limestone deposit in the Martin Bridge formation (Walker, G. W., *Reconnaissance Map of the Oregon Part of the Grangeville Quadrangle, Baker, Union, Umatilla and Wallowa Counties, Oregon*. U.S. Geological Survey, Denver, 1979). A rocky bowl and a line of north-facing cliffs are found on the south side of the stream between 2280 and 2320 meters. The steeply angled limestone is shaded in the noon sun of August. Among the cool crevices, vertical cracks and overhanging ledges were 47 rosettes of *A. viride*.

The site is near the treeline, and some scrub conifers grow around the cliffs. Green spleenwort was growing with *Campanula rotundifolia* L., *Cystopteris fragilis* (L.) Bernh., *Pellaea breweri* D. Eaton, *Polystichum lonchitis* (L.) Roth, *Potentilla fruticosa* L., *Salix vestita* Pursh, *Saxifraga oppositifolia* L., *Thalictrum occidentale* Gray, *Valeriana sitchensis* Bong., and *Zigadenus elegans* Pursh.

Though speculative, it is possible the 1987 station could be the same as the 1908 station. But this raises two questions. First, why is the 1908 report from 460 meters higher? Cusick's herbarium labels show he frequently overestimated elevations in the Wallowas. The poor maps of his day would account for this. Second, how could Cusick confuse limestone with granite? Both rocks are common and similarly colored in the Wallowas. Cusick may simply have guessed wrong about the substrate.

The apparent rarity of green spleenwort both in 1908 and 1987 is circumstantial evidence that the two stations could be the same. Cusick

botanized in the Wallowas for years (he lived nearby) and only collected the species once. The recent search of each of the four forks of the Imnaha River yielded only one site. Spleenwort habitat, shady north-facing limy ledges at timberline, is scarce in the Imnaha drainage. Unsuccessful attempts were also made to locate *A. viride* in 1987 in the limy Hurricane Creek, Wallowa River, and Frances Lake basins of the Wallowas.

Green spleenwort has a circumboreal range and is too common in the northern United States for federal threatened or endangered status under the Federal Endangered Species Act as amended. Green spleenwort can not be considered threatened or endangered within Oregon at this time, according to current state statutes. The Oregon colony is distant from the nearest roads and hiking trails, and therefore remote from their implied threats. Although the U.S. Forest Service allows domestic sheep and horse grazing in the Eagle Cap Wilderness, the *Asplenium* is not threatened or endangered by grazing since it grows on inaccessible cliffs. However, the solitary population is small and disjunct, and thus should remain on the Oregon and Wallowa-Whitman National Forest sensitive species lists. Because the *A. viride* population is small, I limited my voucher (*Zika 10431* ORE, OSC) to a few fronds from large plants and did not uproot rosettes.

I thank the Oregon Natural Heritage Data Base and the Wallowa-Whitman National forest for supporting this field work.—PETER F. ZIKA, District Botanist, Bureau of Land Management, Eugene District, PO Box 10226, Eugene, Oregon 97440.

Seven Clubmosses New to Arkansas.—Until recently, only *Lycopodium lucidulum* and *L. appressum* were known to occur in Arkansas (Taylor & Demaree, Rhodora 81:503–548, 1979). *Lycopodium lucidulum* Michx., first reported by Bowers and Redfearn (Amer. Fern J. 57:91–92), 81:503–548, 1979), is represented in Arkansas by several populations in the Boston Mountains that are extreme southwestern disjuncts from the species' metropolis in northern and eastern North American. In contrast, *L. appressum* (A. Chapman) F. Lloyd & L. Underw., is widely dispersed to the south along the Gulf Coastal Plain, but in Arkansas, it was known (Taylor & Demaree, Rhodora 81:503–548, 1979) from only five southcentral counties (Clark, Hempstead, Ouachita, Saline, and Union cos.). During the last three years (1985–1987), collectors encountered four *Lycopodium* species and three interspecific hybrids that are new to the Arkansas flora. In addition, they located *L. appressum* in two more counties (Calhoun and Hot Spring cos.). These discoveries significantly increase the number of species and distribution of *Lycopodium* in Arkansas.

Lycopodium digitatum A. Braun was collected in Arkansas for the first time from Benton Co. on 11 Nov 1987. Edwin B. Smith, curator of the herbarium at the University of Arkansas at Fayetteville kindly sent the voucher (*Mottesheard* 55, UARK) to us for verification. The plant was located on a slope within pine/hardwood forest, 5–7 km ESE of Siloam Springs. No other representative from *Lycopodium* sect. *Diphasium* is known from Arkansas. This population is

disjunct 400 km from its nearest populations to the north in Iowa and Illinois (Peck, Contr. Milwaukee Pub. Mus. Geol. Biol. 53:1–143, 1982) and to the east in Kentucky (Johnson & McCoy, Amer. Fern J. 65:29, 1975).

Three *Lycopodium* species and three interspecific hybrids new to Arkansas were discovered in 1985 and 1986 by C. Amason, E. Bridges, S. Orzell, C. J. Peck, and J. H. Peck. While inspecting eight *L. appressum* colonies located by Amason in Calhoun Co., it was noted that these populations contained additional *Lycopodium* taxa (Orzell & Bridges, Phytologia 64:81–144, 1987). This discovery led to a search that located 14 more colonies in Calhoun Co. Analysis of these populations resulted in the addition of six taxa to the vascular flora of Arkansas. Growing with *L. appressum* were the species *L. carolinianum* L., *L. alopecuroides* L., and *L. prostratum* Harper and their hybrids *L.* ×*bruceii* Lellinger (*L. appressum* × *prostratum*), *L.* ×*copelandii* Eiger (*L. alopecuroides* × *appressum*), and *L. alopecuroides* × *prostratum*. The populations were found at disturbed sites with moist sand or clay soil, such as graded timber-access road ditches, pine plantation reforestation sites, barrow pit ponds, and gravel pit operations. The authors' voucher specimens are deposited in the herbarium of the University of Arkansas at Little Rock (LRU).

The phenomenon of many taxa of a pteridophyte genus commonly growing together, recently known as a "genus community" (Wagner & Wagner, Taxon 32:53–62, 1983), provides an ideal opportunity to compare and contrast species of a genus that are difficult to identify when found growing alone. A difficulty in identification exists with respect to members of the *L. inundatum* complex in the Gulf Coastal Plain where they are reported as commonly occurring in genus communities (Bruce, Univ. Microfilm 76–9355, 1975). Observations of a *Lycopodium* community in neighboring Kentucky (Johnson & McCoy, loc. cit.; Cranfill, Amer. Fern J. 71:97–100, 1981) suggest that *L. appressum* and its hybrids may be more winter-hardy than *L. alopecuroides* and *L. prostratum*. In that all parents and hybrids were found in Arkansas, we suggest either that the colonization process is more recent in Arkansas, or that the residence time of winter-sensitive parental species may be more prolonged in Arkansas. In either case, the Arkansas populations provide exceptional opportunities for comparative studies of long-term population events among the species and their hybrids.—James H. Peck and Carol J. Peck, Biology Department and Office of Testing and Student Life Research, University of Arkansas–Little Rock, Little Rock, Arkansas 72204.

REVIEWS

"Bibliografía comentada sobre pteridofitas de México," by Ramón Riba and Armando Butanda. 1987. 88 pp. Consejo Nacional de la Flora de México, Apartado Postal 17-584, Delagación Miguel Hidalgo, 11410 México, D.F. $10.00 U.S. (incl. postage). ISBN 968-6144-02-1.

Fern enthusiasts will find this extensive bibliography listing the publications on Mexican pteridophytes for the last 25 years (since publication of *An annotated bibliography of Mexican ferns*, by G. N. Jones, 1966) extremely useful. Most citations are followed by a short note indicating their contents. Following the Introduction, there is a catalogue of the books and periodicals used in the bibliography. The 56 pages of citations are followed by these very useful indices: Bibliographies, lists and glossaries; Ethno-botany; Geography: States of Mexico; Geography: Countries and regions of America; Systematics; Vegetation and Floristic Studies. The seven pages of an index to authors is followed by three pages of additional citations. The authors are to be commended for making this very valuable tool available to all botanists.—A. J. SHARP, Department of Botany, University of Tennessee, Knoxville, Tennessee 37996.

"Liebmann's Mexican ferns: His itinerary, a translation of his 'Mexicos Bregner,' and a reprinting of the original work," by John T. Mickel with contributions by Rogers McVaugh, Sven Karell, and Henrik Balslev. 1987. 350 pp. Contr. New York Bot. Gard. 19. Available from Scientific Publications Office, New York Botanical Garden, Bronx, NY 10458. $30.50 (U.S.), $31.50 (non-U.S.), paperbound. USBN 0-89327-324-4.

Although Liebmann's (1849) work on the ferns of southern Mexico (Puebla, Veracruz, and Oaxaca) is largely outdated taxonomically as a result of modern accounts, it is still important from an historical perspective to study his collections, itinerary, and published work in order properly to afix names to collections. Most of the publication by Mickel et al. is an English translation of Liebmann's work and a reprinting of the original Danish version (*Mexicos Bregner, en systematisk, critisk, plantgeographisk Undersögelse*. Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., V. 1:151–322. 1849). The translation contains the modern names (according to Mickel) of the plants treated by Liebmann and an index to all names, both present-day and those used by Liebmann. What makes this work most useful is a discussion by McVaugh of Liebmann's itinerary and a gazetteer of localities given in Liebmann's published work and on his collections in Copenhagen. Many of these localities are obscure (some no longer extant), not found on modern maps, and never again revisited by botanists, who nowadays often travel by car rather than by foot. McVaugh's unequaled knowledge of the travels of early botanists in Mexico will be essential to anyone trying to localize one of Liebmann's collections. This book will be welcomed by all who deal with plants of southern Mexico and by those interested in early botanical narrative.—ALAN R. SMITH, Herbarium-Department of Botany, University of California, Berkeley, California 94720.

"*Monograph of the Neotropical fern genus* Polybotrya (*Dryopteridaceae*)," by R. C. Moran. 1987. Illinois Natural History Survey Bulletin 34(1): 1–138. ISSN 0073-4918. Available free of charge from the Illinois Natural History Survey, Natural Resources Building, 607 East Peabody Drive, Champaign, Illinois 61820, USA.

From an unlikely source, the Illinois Natural History Survey, comes an excellent new work on Neotropical ferns: a revision of the 35 species of the hemiepiphytic/climbing-fern genus *Polybotrya*, by R. C. Moran, currently of the Missouri Botanical Garden. The work follows a traditional monograph format, with discussions of taxonomic history, ecology, geography, morphology and anatomy, and phylogeny preceding the key and descriptions. All species accounts include synonymy, full descriptions, citation of published illustrations, discussion, and citation of specimens; each account is accompanied by a clear and detailed full-page line drawing by the author. Ten new species are described. A bibliography, distribution maps, a list of exsiccatae, and a general index complete the volume.

I found that the monograph provided for easy identification of specimens. The key is straightforward, once some specialized terms have been mastered by the user, and recondite characters are illustrated. The key emphasizes characters of the sterile leaves (in fact, sterile material is required for many of the leads), and you can get to couplet 37 (out of 42) on sterile material alone. When the key did not bring a positive determination, I was able to make an identification by matching my specimen with an illustration. A listing of species by country (p. 10) is another handy identification aid.

In the section on Morphology and Anatomy are recounted some of the unusual biological aspects of Polybotrya species, such as the presence of aerophores and mucilage on the rhizome and petiole, and presence of nectaries on the rachis (previously known for *P. osmundacea*, but here also reported for *P. alfredii*). I was disappointed, however, that no descriptions were given of *Polybotrya* gametophytes, even from cultured spores. The section on Ecology was brief, regrettable in view of the author's extensive field experience with most of the species, and the section on Geography would have been more illuminating if the described patterns had been examined in light of the author's proposed phylogeny (p. 31) of the species of *Polybotrya*. Moran's phylogenetic conclusions concerning *Polybotrya* contain some surprises: the members of the distinctive segregate genus *Soromanes* are highly specialized polybotryas, the terrestrial habit of *P. sorbifolia* and *P. fractiserialis* is derived within the genus from a hemiepiphytic one, and the closest relative of *Polybotrya* and its monotypic sister genus *Olfersia* is probably *Cyclodium*, not *Maxonia* as many earlier authors have proposed. Ample data are presented to provide hours of cladistic entertainment.

There is no reason for anyone interested in the taxonomy of ferns not to own this book. As stated on the copyright page, "Single copies of most publications [of the Illinois Natural History Survey] are available to anyone requesting them." Write for your copy today.—David M. Johnson, New York Botanical Garden, Bronx, New York 10458.

INFORMATION FOR AUTHORS

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American Fern Journal 78(3): 77–85 (1988)

Taxonomic and Phytogeographic Relationships of *Diplazium flavoviride, D. pycnocarpon,* and *Diplaziopsis*

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Diplazium, a worldwide genus of about 400 species, is the largest genus of the athyrioid group, although Ching (1964b) placed the majority of species of *Diplazium* in the genus *Allantodia*. Several monotypic or oligospecific genera, such as *Callipteris, Dictyodroma, Diplaziopsis, Hemidictyum,* and *Monomelangium*, are often segregated from *Diplazium* and recognized on the basis of a few specialized characters (Copeland, 1947; Crabbe et al., 1975; Ching, 1978). All of these are closely related to and probably derived from *Diplazium*. *Diplaziopsis*, comprising two species, is defined by its pinnate leaves with a conform terminal pinna, thin lamina texture, anastomosing veins, and sausage-like sori (Copeland, 1947). Ching (1964a) added two new species from China to *Diplaziopsis*.

Diplazium flavoviride was described by Alston (1940a, 1940b) from New Guinea. He noted "[it is] Apparently allied to the North American *Athyrium pycnocarpon* (Spreng.) Tidestr., which as pointed out by Butters (Rhodora XIX, p. 178 (1917)), should be referred to *Diplazium* as *D. pycnocarpon* (Spreng.) Broun." However, *D. flavoviride* has not been given attention in later studies of the taxonomic and phytogeographic relationships of *D. pycnocarpon*, which was compared only with *Diplaziopsis* (Tryon & Tryon, 1973; Kato & Iwatsuki, 1984). *Diplazium pycnocarpon* is commonly referred to *Athyrium* by many North American pteridologists who otherwise recognize *Diplazium* as distinct from *Athyrium* (e.g., Morton, 1968; Mickel, 1979; Lellinger, 1985).

The intercontinentally discontinuous distribution of identical or closely related taxa of plants between eastern North America and eastern Asia, extending to southern and southeastern Asia in some cases, is a classic and well-known example of disjunct distribution patterns (Li, 1952; Graham, 1972), referred to as a Tertiary relict disjunction (Wood, 1972). Tryon and Tryon (1973) and Kato and Iwatsuki (1984) included *Diplazium pycnocarpon* and *Diplaziopsis* among the pairs vicariant between the two regions. Boufford and Spongberg (1984) note "our knowledge and understanding of the eastern North American–eastern Asian floristic connection will in large measure reflect and be determined by our knowledge of the systematics of the taxa involved."

In this study we examine the taxonomic relationship of *Diplazium flavoviride* and *D. pycnocarpon*, and also that between these two species and the segregate

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FIG. 1. *Diplazium flavoviride*. A, Seram specimen with erect rhizome and lanceolate leaf, × .42. Arrows indicate reduced basal pinnae. B, Cleared fertile pinna, × 5.5.

genus *Diplaziopsis*. On the basis of the taxonomic relationships, we discuss the phytogeographic relationship of these species.

Materials and Methods

In this study we used living material of *D. flavoviride*, *D. pycnocarpon*, and *Diplaziopsis cavaleriana* (Christ) C. Chr. cultivated in the Botanical Gardens, Faculty of Science, University of Tokyo, and also dried and pickled specimens of these species and *Diplaziopsis javanica* (Blume) C. Chr. The material of *Diplazium flavoviride* was originally collected from Seram (Ceram) Island, the Moluccas, east of New Guinea. For examination of veins, pinnae were cleared in commercial bleach and stained with 1% basic fuchsin solution. Rachises were sectioned with a freezing microtome to examine the cross sections of the adaxial grooves. For cytological study, root tips of *D. flavoviride* were pretreated with 0.02M 8–hydroxyquinoline solution, kept in a dark room at 20° C for three hours, separated from the root cap, fixed in 45% acetic acid for 2–3 minutes, stained with 2% aceto-orcein solution, and squashed. Spore size was measured in 100 spores from one specimen of each species. For scanning electron microscopy (SEM) of spores, untreated spores were coated with gold and observed under an Hitachi S–700. Voucher specimens of the four species examined are deposited in the herbarium of the University of Tokyo (TI).

Results

Diplazium pycnocarpon and the species of *Diplaziopsis* are well known ferns, and their gross morphologies have been described by many workers (for *D. pycnocarpon*, Morton, 1968; Mickel, 1979; Lellinger, 1985; for *Diplaziopsis*, Sledge, 1962; Ching, 1964a; Ohwi, 1965). Although *Diplazium flavoviride* is relatively little known, its characters were fully described with a photograph by Alston (1940a, 1940b). Therefore, the following descriptions concentrate on poorly known characters.

Habitat and habit. — *Diplaziopsis* species and *Diplazium pycnocarpon* are terrestrial on wet ground or slopes in shade of tropical montane forests at 1000–2000 m *(Diplaziopsis javanica)*, warm-temperate *(Diplaziopsis cavaleriana)*, and temperate *(D. pycnocarpon)* woods. *Diplazium flavoviride* is a lithophyte growing on mossy limestone rocks in light shade in tropical, mossy montane forests at about 2000 m on Seram Island (1500–1800 m in New Guinea). The plants have erect or suberect rhizomes bearing 3–5 clustered leaves with curved rachises and obliquely downward pointing lamina tips, and many stipe-bases not so prominent as in *D. pycnocarpon* (Johnson, 1986).

Lamina. — The leaf lamina of all four species is pinnate and thin-herbaceous. The pinnae are entire and truncate or subauricled at the acroscopic base (Fig. 1). The lower pinnae are somewhat reduced. The lamina is gradually narrowed toward the narrow-deltoid, lobed apex in the very similar *D. flavoviride* and *D. pycnocarpon* (Fig. 2), while it has a terminal pinna conforming to the lateral pinnae in *Diplaziopsis*.

FIG. 2. Apical part of leaf in *Diplazium* species. A, *Diplazium flavoviride*. B, *D. pycnocarpon*. A, B, × 1.0.

Rachis. — The rachis as well as the stipe is terete on the abaxial side and grooved adaxially in the four species. The groove is V-shaped in cross section in *Diplazium flavoviride*, *D. pycnocarpon* and *Diplaziopsis*. It is U-shaped with a flat bottom in the *Diplazium dilatatum* group, the major infrageneric group of *Diplazium* (Kato, 1977), to which *D. mettenianum* is referred (Fig. 3).

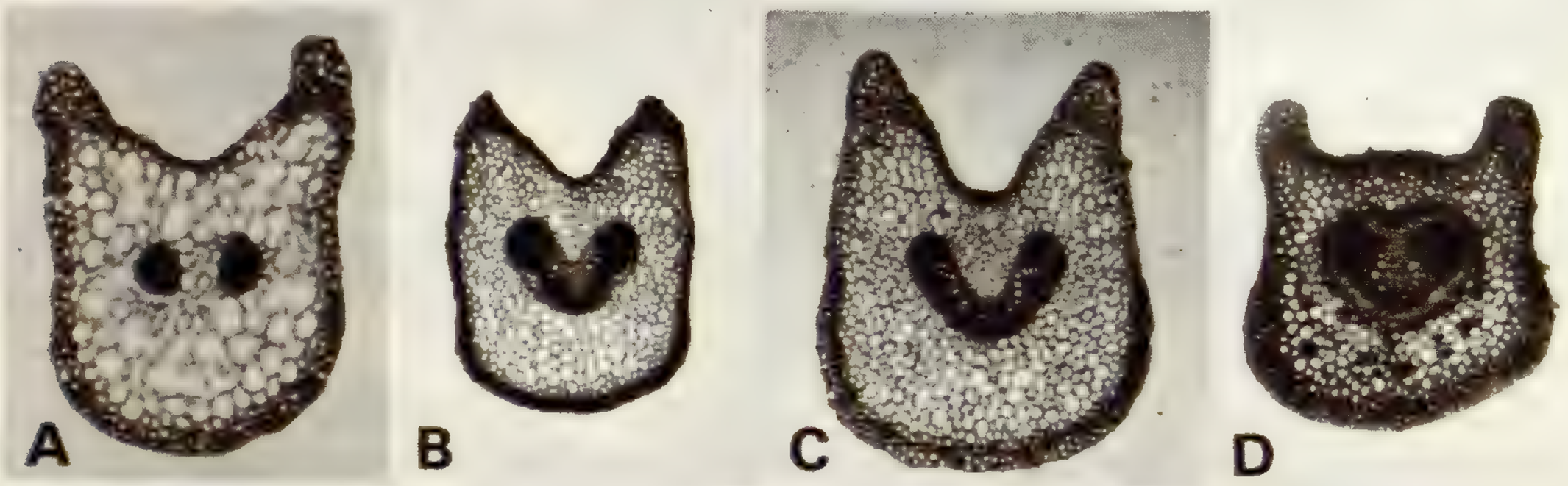

FIG. 3. Cross sections of rachis in *Diplazium* and *Diplaziopsis*. A, *Diplazium flavoviride*, × 25. B, *D. pycnocarpon*, × 17. C, *Diplaziopsis cavaleriana*, × 17. D, *Diplazium mettenianum*, × 14.

Veins and sori. —Veins are free with usually once-forked lateral veins reaching nearly to the barely crenulate pinna-margin in *D. flavoviride* and *D. pycnocarpon*, although the crenulation is more regular in the latter species (Fig. 4A, B). In *Diplaziopsis* the veins are sagenioid-anastomosing, i.e., having elongate areoles with no included free veinlets, and vein-endings, whether free or areolate, ending well short of the entire or subundulate lamina margin (Fig. 4C). Sori are elongate and thick with vaulted, more or less thick or thin *(Diplaziopsis)* indusia in all four species.

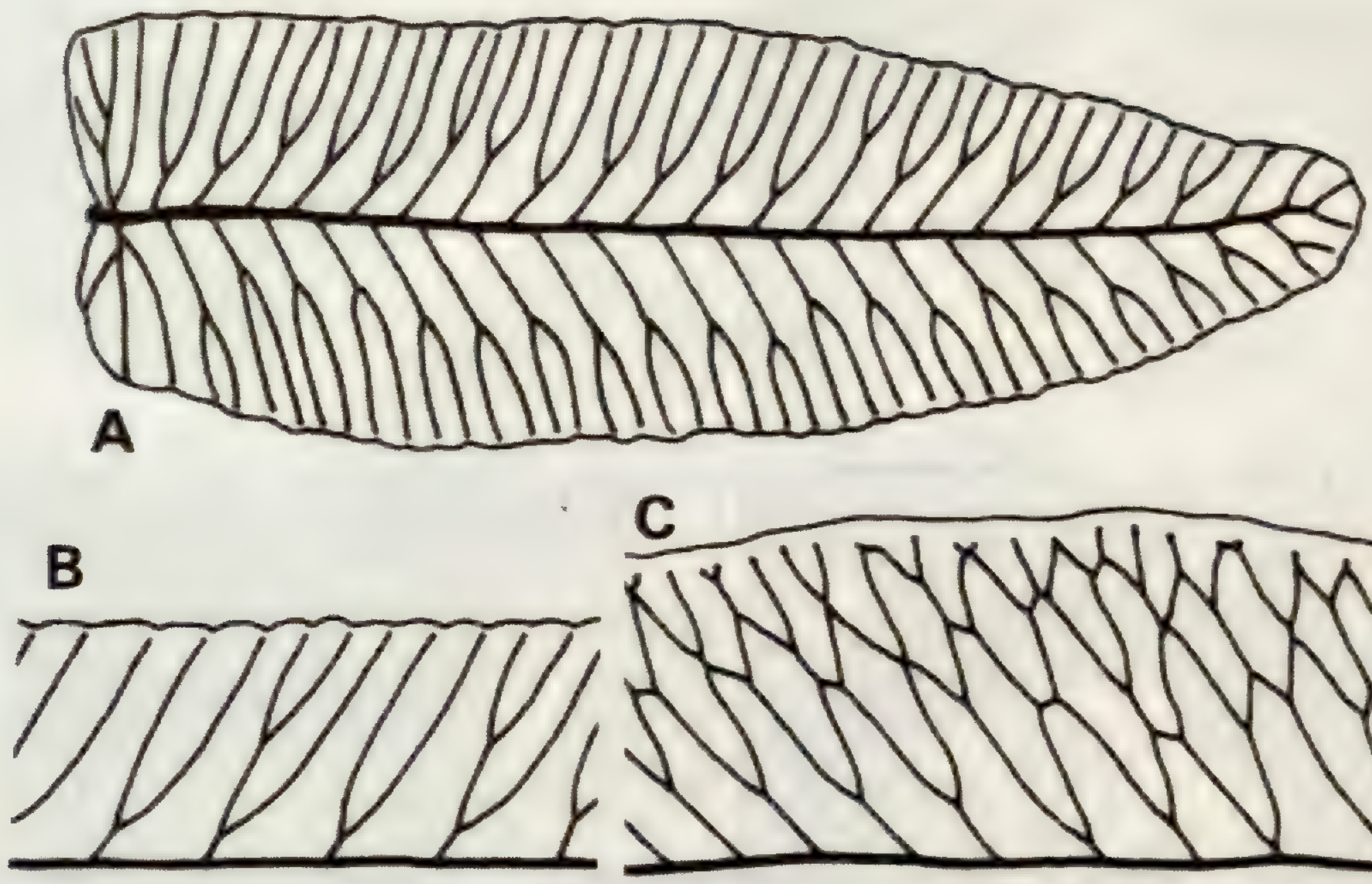

FIG. 4. Venation in *Diplazium* and *Diplaziopsis*. A, *Diplazium flavoviride*, × 2.7. B, *D. pycnocarpon*, × 2.4. C, *Diplaziopsis javanica*, × 2.7.

Spores. — Spores of the four species are monolete and subglobose (Fig. 5). They are dark brown in *D. pycnocarpon*, and brown in the other three species. The diameter (excluding perispore) is 30–40 (mean, 35.3) × 25–35 (30.7) μm in *D. flavoviride*, 25–36 (31.2) × 23–29 (25.5) μm in *D. pycnocarpon*, 28–43 (35.0) × 20–31 (27.1) μm in *Diplaziopsis javanica*, and 23–33 (30.2) × 20–25 (22.0) μm in *Diplaziopsis cavaleriana*. The perispore of all four species is winglike in light microscopy, and lophate with convolute or echinate projections on the lumina in SEM. The height of the perispore is up to 8 μm in *D. flavoviride*, 3 μm in *D. pycnocarpon*, 8 μm in *Diplaziopsis javanica*, and 6μm in *Diplaziopsis cavaleriana*. The perispore bears fine reticulate ornamentations on the surface in *D. flavoviride* and *D. pycnocarpon* (Fig. 5A–D). Such ornamentations are rather poorly developed in *Diplaziopsis javanica* (Fig. 5E, F), while they are more finely reticulate or scaly-reticulate in *Diplaziopsis cavaleriana* (Fig. 5G, H).

Chromosomes. — *Diplazium flavoviride* has 80 chromosomes in somatic cells examined at mitosis (Fig. 6), the same number as that reported for *D. pycnocarpon* (Löve et al., 1977).

TAXONOMIC RELATIONSHIPS

Comparisons in almost all characters described above as well as in others such as scales, leaf size, and stipes (Alston, 1940a, 1940b) show remarkable similarities between *D. flavoviride* and *D. pycnocarpon*. They include not only such leaf characters as leaf shape, texture, pinna shape, rachis-grooves, veins, and sori, but also spore morphology and chromosome number. A recent work

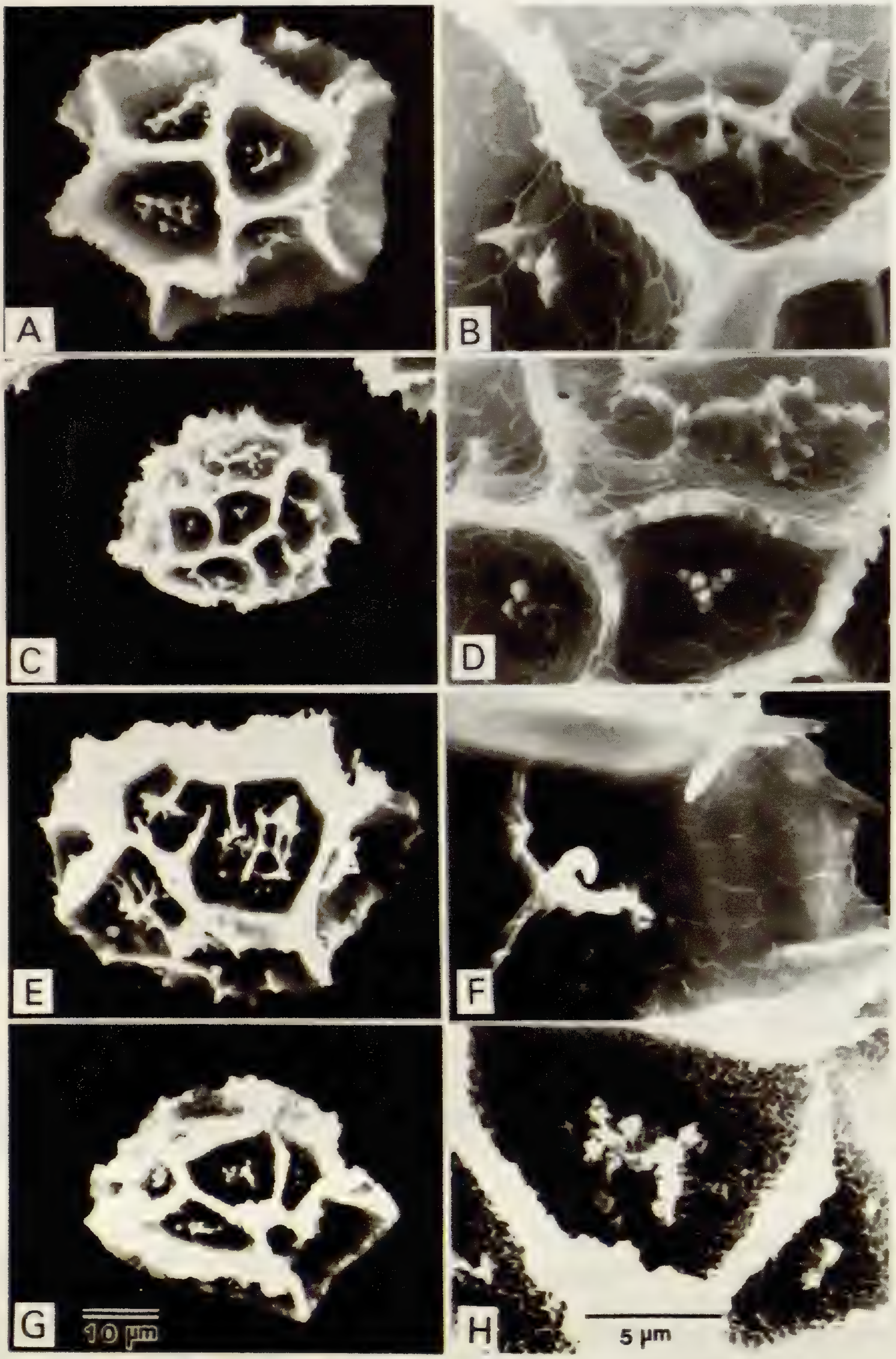

FIG. 5. SEM photographs of *Diplazium* and *Diplaziopsis* spores. A, B, *Diplazium flavoviride*. C, D, *D. pycnocarpon*. E, F, *Diplaziopsis javanica*. G, H, *Diplaziopsis cavaleriana*. A, C, and E magnified as in G; B, D, and F magnified as in H.

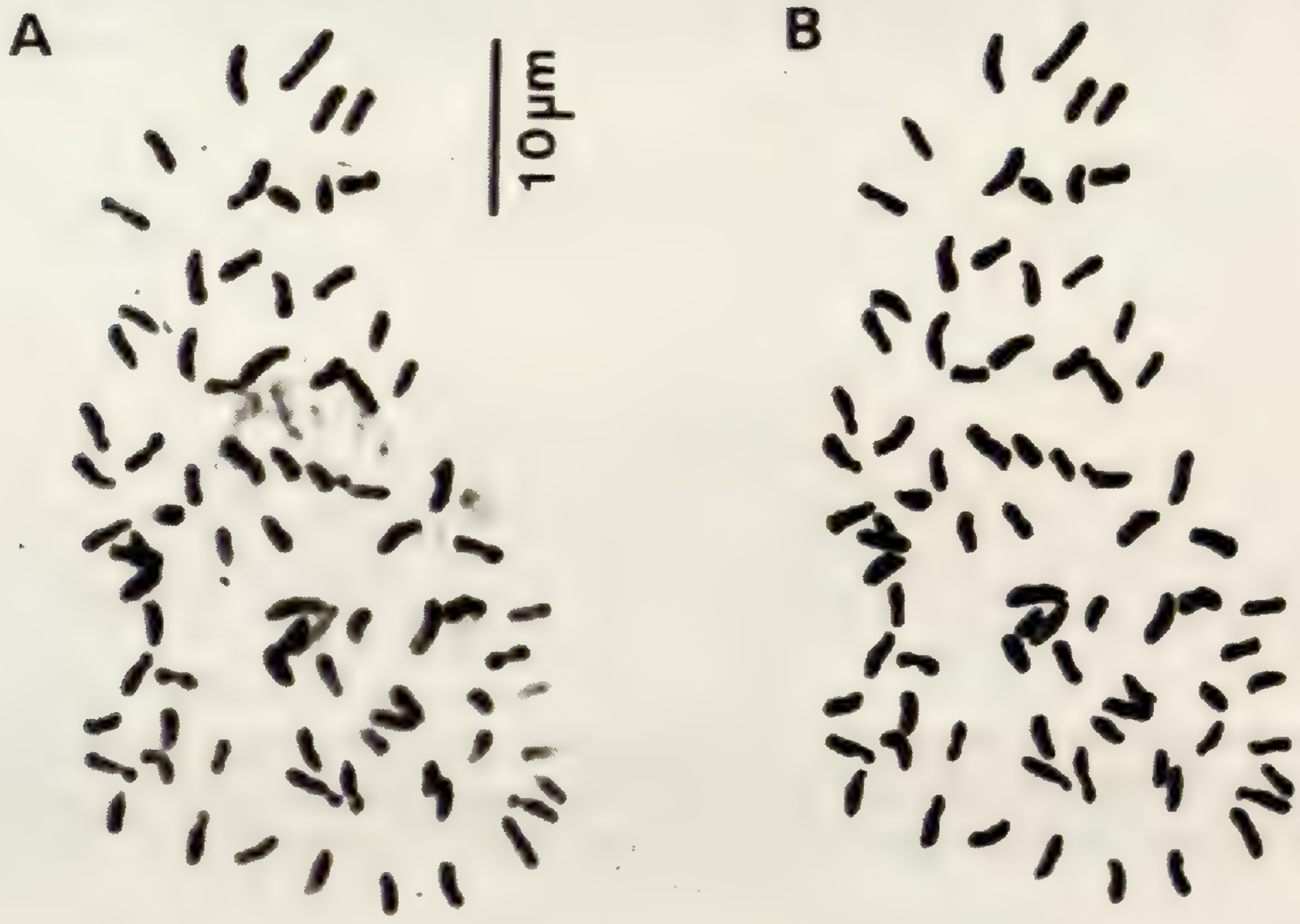

FIG. 6. Somatic chromosomes ($2n = 80$) of *Diplazium flavoviride*. A, Photograph. B, Interpretative drawing.

(Nakato & Mitui, 1979) showed that *Diplazium* has chromosome numbers of $x = 41$, and also $x = 40$, rarely. Thus the shared chromosome number is a derived character that may suggest a close taxonomic relationship. Among the common characters, furthermore, the cross sections of rachis-grooves are useful to define the infrageneric groups of *Diplazium* (Kato, 1977). A combination of those characters suggests a close relationship between the two species, as correctly noted by Alston (1940a, 1940b). Although *D. pycnocarpon* is commonly referred to *Athyrium* (Morton, 1968; Mickel, 1979; Lellinger, 1985), it seems to be a temperate *Diplazium* species. *Diplazium pycnocarpon* has none of the characteristic features of *Athyrium* such as swollen stipe-bases, adaxial spines at the bases of costae and costules, pale, cartilaginous edge of lamina, and curved sori (Kato, 1977).

Differences between the two species include rhizome habit (erect in *D. flavoviride* and creeping in *D. pycnocarpon*) and dimorphism (not apparently dimorphic in *D. flavoviride* and subdimorphic in *D. pycnocarpon*). Johnson (1986) pointed out that *D. pycnocarpon* has starch-containing, persistent stipe-bases; these are not prominent in *D. flavoviride*.

Diplazium flavoviride and *D. pycnocarpon* are also closely related to *Diplaziopsis*, as pointed out by Tryon and Tryon (1973) and Kato and Iwatsuki (1984). This is suggested by their similar pinna shape, rachis-grooving, indusia,

and spores, although they are different in lamina apex, venation, and the chromosome number (Löve et al., 1977). While the first two are derived characters of *Diplaziopsis*, the last (x = 41) is shared between it and the bulk of *Diplazium*. The overall similarities lead us to conclude that *Diplaziopsis*, even though quite different from *Diplazium* in a few obvious characters, should be treated as an infrageneric group of the latter genus, as done by Kato (1977). A *Diplazium* from which *Diplaziopsis* is excluded would be a paraphyletic taxon still including species closely related to *Diplaziopsis*. No nomenclatural or taxonomic ranking for this group is given here, pending further work on a natural infrageneric classification of *Diplazium*.

Phytogeographic Relationship

The disjunct distributions between eastern North America and eastern Asia are not only demonstrated by many flowering plants (Li, 1952), but also by some pteridophytes (Tryon & Tryon, 1973; Kato & Iwatsuki, 1984). *Diplazium pycnocarpon* and the species of *Diplaziopsis* have been cited as examples of this by Tryon and Tryon (1973) and Kato and Iwatsuki (1984). However, the real vicarious pair of species are, as discussed above, *D. flavoviride* of eastern Malesia and *D. pycnocarpon* of eastern North America (Fig. 7). Although such a distribution is somewhat aberrant, compared to the common eastern North American-eastern Asian distribution pattern, the *Diplaziopsis* group including the two species of *Diplazium* is widely distributed in eastern, southern, and Southeast Asia and in the Pacific islands. A similar distribution pattern is shown by another athyrioid group, *Deparia* sect. *Lunathyrium* (Kato & Iwatsuki, 1984), and somewhat similar patterns are found in some flowering plants such as *Astilbe*, *Gordonia*, *Illicium*, *Itea*, *Lindera* and *Nyssa* (Li, 1952). It seems likely that the distribution pattern of the *Diplaziopsis* group has been affected by the same geological and climatic conditions as the eastern North American–eastern

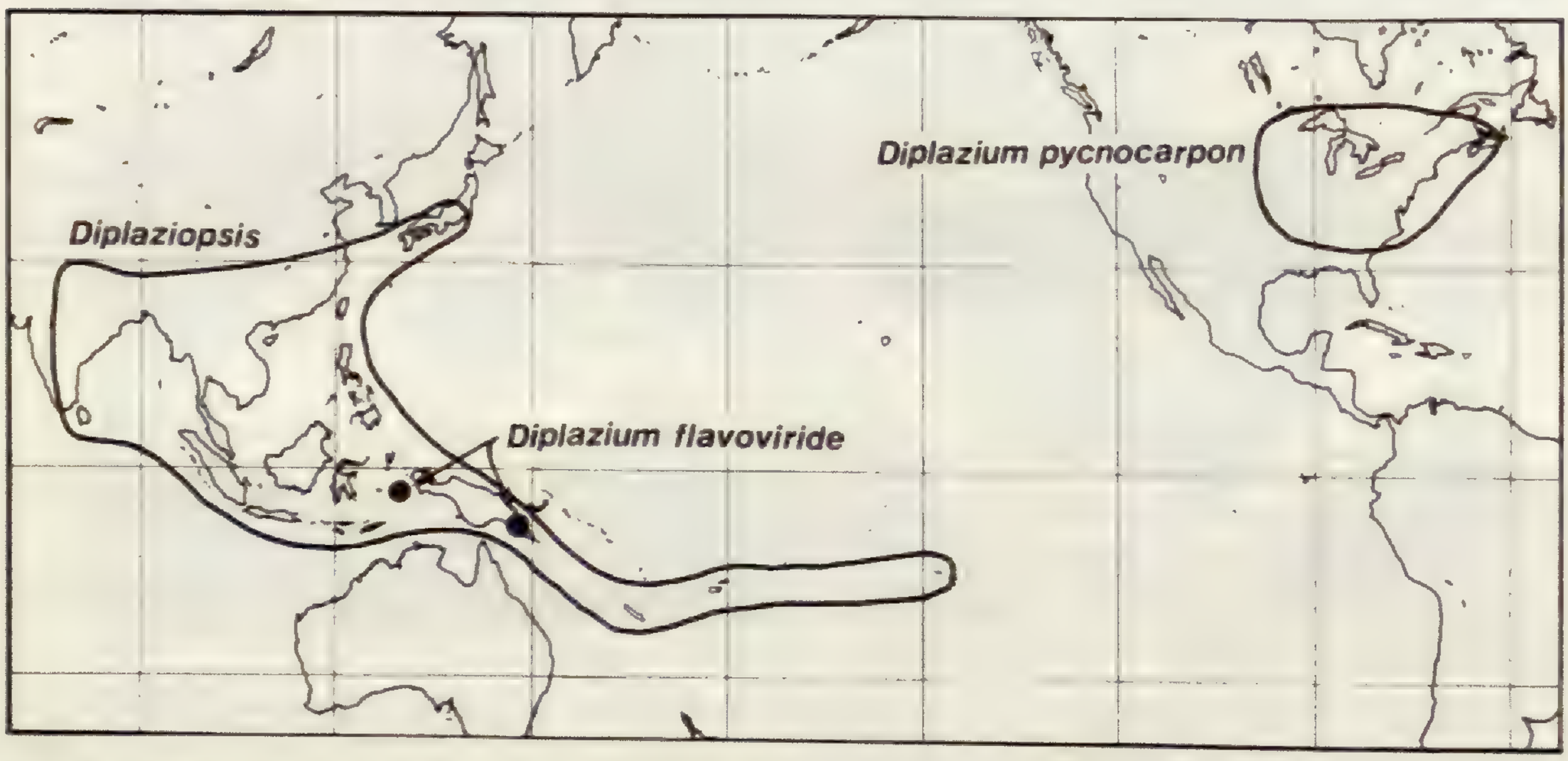

Fig. 7. Distributions of *Diplazium flavoviride*, *D. pycnocarpon*, and *Diplaziopsis*.

Asian distribution patterns exhibited by many vascular plants. As almost all fern species of Seram Island are Malesian in affinity (Kato, 1987), this amphipacific distribution pattern of the *Diplaziopsis* group is unique.

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Literature Cited

Alston, A. H. G. 1940a. Undescribed ferns from New Guinea. J. Bot. 78:225–229.

———, 1940b. Undescribed ferns from New Guinea. Nova Guinea, n.s., 4:109–112.

Boufford, D. E. and S. A. Spongberg. 1984. Eastern Asian–eastern North American phytogeographical relationship—a history from the time of Linnaeus to the twentieth century. Ann. Missouri Bot. Gard. 70:423–439.

Ching, R.–C. 1964a. On the genus *Diplaziopsis* C. Chr. Acta Phytotax. Sin. 9:31–36.

———, 1964b. On some confused genera of the family Athyriaceae. Acta Phytotax. Sin. 9:41–84.

———, 1978. The Chinese fern families and genera: systematic arrangement and historical origin. Acta Phytotax. Sin. 16(3):1–19, 16(4):16–37.

Copeland, E. B. 1947. *Genera filicum*. Waltham, Mass.: Chronica Botanica.

Crabbe, J. A., A. C. Jermy, and J. T. Mickel. 1975. A new generic sequence for the pteridophyte herbarium. Fern Gaz. 11:141–162

Graham, A. (ed.). 1972. *Floristics and paleofloristics of Asia and eastern North America*. Amsterdam: Elsevier.

Johnson, D. M. 1986. Trophopods in North American species of *Athyrium* (Aspleniaceae). Syst. Bot. 11:26–31.

Kato, M. 1977. Classification of *Athyrium* and allied genera of Japan. Bot. Mag. Tokyo 90:23–40.

———, 1987. Floristic richness and phytogeography of Seram pteridophytes. Acta Phytotax. Geobot. 38:57–62. (in Japanese)

——— and K. Iwatsuki. 1984. Phytogeographic relationships of pteridophytes between temperate North America and Japan. Ann. Missouri Bot. Gard. 70:724–733.

Lellinger, D. B. 1985. *A field manual of the ferns and fern-allies of the United States & Canada*. Washington, D.C.: Smithsonian Inst. Press.

Li, H.–L. 1952. Floristic relationships between eastern Asia and eastern North America. Trans. Amer. Philos. Soc. 42:371–429. (Reprinted as: Morris Arboretum Monograph Edition. 1971. With a foreward and additional literature citation i–ii. Original pagination retained.)

Löve, A., D. Löve, and R. E. G. Pichi Sermolli. 1977. *Cytotaxonomical atlas of the Pteridophyta*. Vaduz: J. Cramer.

Mickel, J. T. 1979. *How to know the ferns and fern allies*. Dubuque, Iowa: Wm. C. Brown.

Morton, C. V. 1968. Pteridophyta. Pp. 1–57 in H. A. Gleason, *The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada*, Vol. 1. New York: Hafner.

Nakato, N. and K. Mitui. 1979. Intraspecific polyploidy in *Diplazium subsinuatum* (Wall.) Tagawa. J. Jap. Bot. 54:129–136.

Ohwi, J. 1965. *Flora of Japan*. Washington, D.C.: Smithsonian Institution.

Sledge, W. A. 1962. The athyrioid ferns of Ceylon. Bull. Brit. Mus. (Nat. Hist.), Bot. 2:277–323.

Tryon, A. F. and R. M. Tryon. 1973. *Thelypteris* in northeastern North America. Amer. Fern J. 63:65–76.

Wood, C. E. Jr. 1972. Morphology and phytogeography: the classical approach to the study of disjunctions. Ann. Missouri Bot. Gard. 59:107–124.

American Fern Journal 78(3): 86–95 (1988)

Calochlaena, a New Genus of Dicksonioid Ferns

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The genus *Culcita* C. Presl contains several species of dicksonioid ferns. Before 1922 these species were included in *Balantium* Kaulf., then regarded as typified by *Balantium culcita* (L'Hér.) Kaulf. (now known as *Culcita macrocarpa* C. Presl). Maxon (1922) demonstrated that *Balantium* should be typified by *B. auricomum* Kaulf., a synonym of *Dicksonia arborescens* L'Hér., the type of *Dicksonia*. *Balantium* is thus a synonym of *Dicksonia*. *Culcita* is the correct name for the segregate genus typified by *Dicksonia culcita L'Hér. (= Balantium culcita)*.

Culcita macrocarpa is found in the Azores, Madeira, Spain, and Portugal (Fraser–Jenkins & Laínz, 1983). It is closely related to *C. coniifolia* (Hook.) Maxon, of tropical America. Also included in *Culcita* are several species from Australasia and the Philippines. This latter group of species was first associated with *Balantium* when Diels (1899) and Copeland (1908, 1909) added the species *Balantium stramineum* (Labill.) Diels, *Balantium dubium* (R. Br.) Copel., and *B. javanicum* (Blume) Copel. to that genus.

Maxon (1922) recognized eight species of *Culcita*. Differences in soral characters led him to create a new subgenus *Calochlaena* for two of these species, the Australian *C. dubia* (R. Br.) Maxon and an alleged new species from Fiji, *C. blepharodes* Maxon, which we believe is a synonym of *C. dubia*. Although Maxon regarded such species as *C. straminea* and *C. javanica* as typical *Culcita*, not *Calochlaena*, more recent authors have enlarged subg. *Calochlaena* to include all of the Australasian species (Copeland, 1947; Holttum & Sen, 1961; Holttum, 1963, 1964). These authors apparently were not aware that this was not Maxon's original subgeneric concept.

Significant differences between members of the two subgenera of *Culcita* have frequently been reported. These include differences in anatomy (Davie, 1918; Holttum, 1963; Holttum & Sen, 1961), in spore morphology (Gastony, 1981), and in chromosome number (Manton in Holttum & Sen, 1961; Manton in Holttum, 1963; Roy & Holttum, 1965). These have prompted suggestions that the genus may need to be divided (Holttum, 1963; Roy & Holttum, 1965; Gastony, 1981; Tryon & Tryon, 1982). The need for taxonomic reassessment of *Culcita* became evident to us in the course of an anatomical survey of the tree ferns (see White, 1984). In the present paper we summarize evidence for the generic distinctness of the two groups and erect a new genus for the species of subg. *Calochlaena*. *Culcita* thus becomes restricted to the two species *C. macrocarpa* and *C. coniifolia*.

MATERIALS AND METHODS

Live and preserved plants of *Culcita (Culcita) coniifolia*, *C. (Calochlaena) straminea*, *C. villosa*, and *C. dubia* were studied in detail, and herbarium

specimens of all species of *Culcita* were examined. Three-dimensional anatomy of the shoot was studied by cinematographic analysis of stems cut with a sliding microtome (Zimmerman & Tomlinson, 1965). The anatomy of sori, stems, petioles, and rachises was investigated using microtome sections of paraffin-embedded samples as well as freehand sections of fresh or preserved material. Some dried leaf fragments bearing sori were expanded in dilute Contrad 70 (Schmid & Turner, 1977) for study. Spores of all species were examined with light microscopy, and spores of *Cucita villosa* and *Oenotrichia novae-guineae* were studied using scanning electron microscopy.

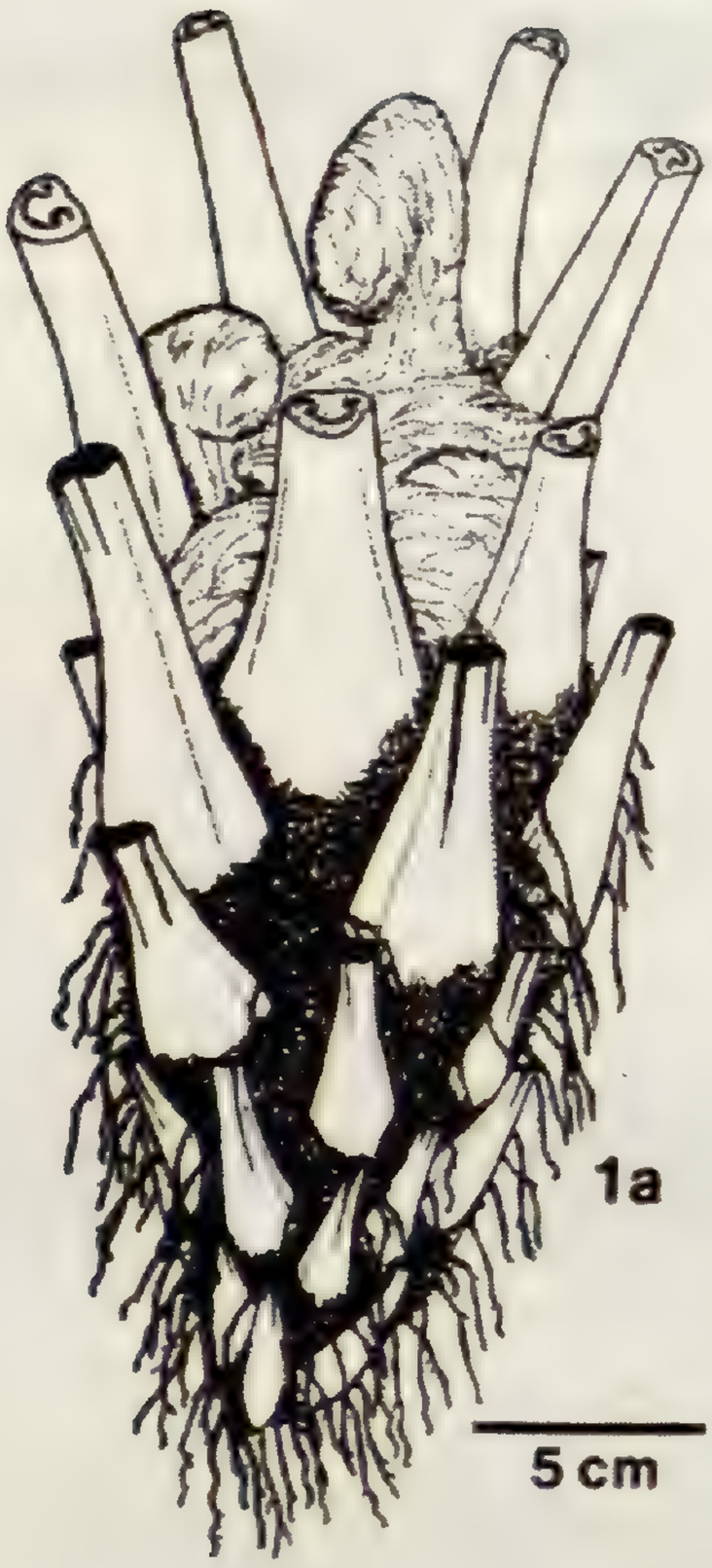
Comparisons

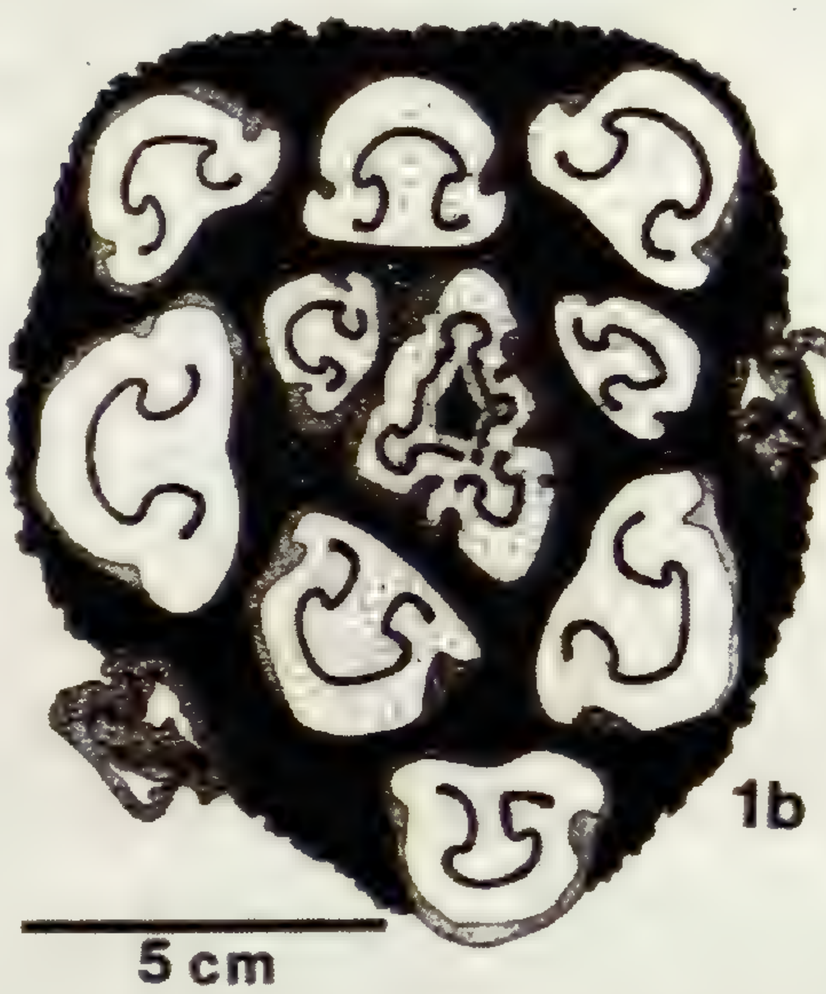
Organography and Anatomy.—Although plants of *C. coniifolia* outwardly appear to have massive short stems similar to the trunks of other tree ferns, sections show that the "trunk" consists of a relatively small erect stem surrounded by persistent petiole bases, hairs, and roots (Fig. 1a, 1b). The enlarged petiole bases contain much starch and together form an imbricated storage organ. Petiolar buds and branches are lacking, although we have seen individuals with dichotomously bifurcated stems. Shoots of subg. *Calochlaena* show a strikingly different pattern. *Culcita straminea* and *C. villosa* have stout horizontally growing rhizomes with distinct nodes and internodes. The rhizomes produce many branches or stolons from lateral buds located on the abaxial sides of the leaf bases (Fig. 2a). The somewhat smaller rhizomes of *C. dubia* are essentially similar to those of the other species. The creeping, branching rhizome systems allow these plants to form extensive clumps through continued vegetative reproduction. References in the literature to arborescent *Calochlaena* (e.g., Copeland, 1909) are probably in error.

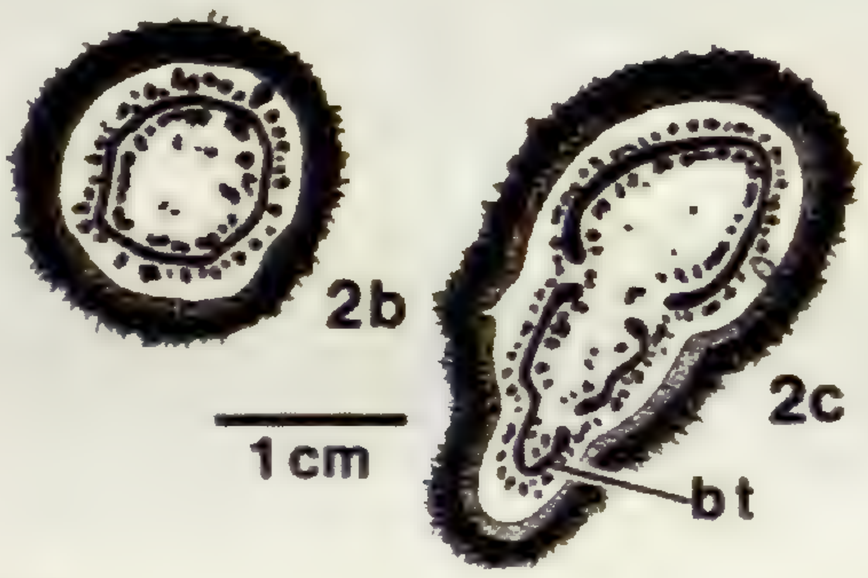
Stems are solenostelic in both subgenera, but the solenosteles are very dissimilar. *Culcita coniifolia* (Figs. 1b, 3) has a relatively small, strongly lobed stele, the lobes decurrent from the insertions of the leaf traces. Leaf positions are close together and the arrangement of leaf gaps approaches the dictyostelic condition. The pith has a sclerenchymatous core from which extend tracelike strands of sclerenchyma associated with the leaf traces (Fig. 3). In the leaf axils the sclerenchyma strands join the sclerenchymatous outer cortex of the stem. No bud or branch traces are found in *Culcita coniifolia*. The figure of Sen (1968) indicates that the stem of *C. macrocarpa* resembles that of *C. coniifolia*.

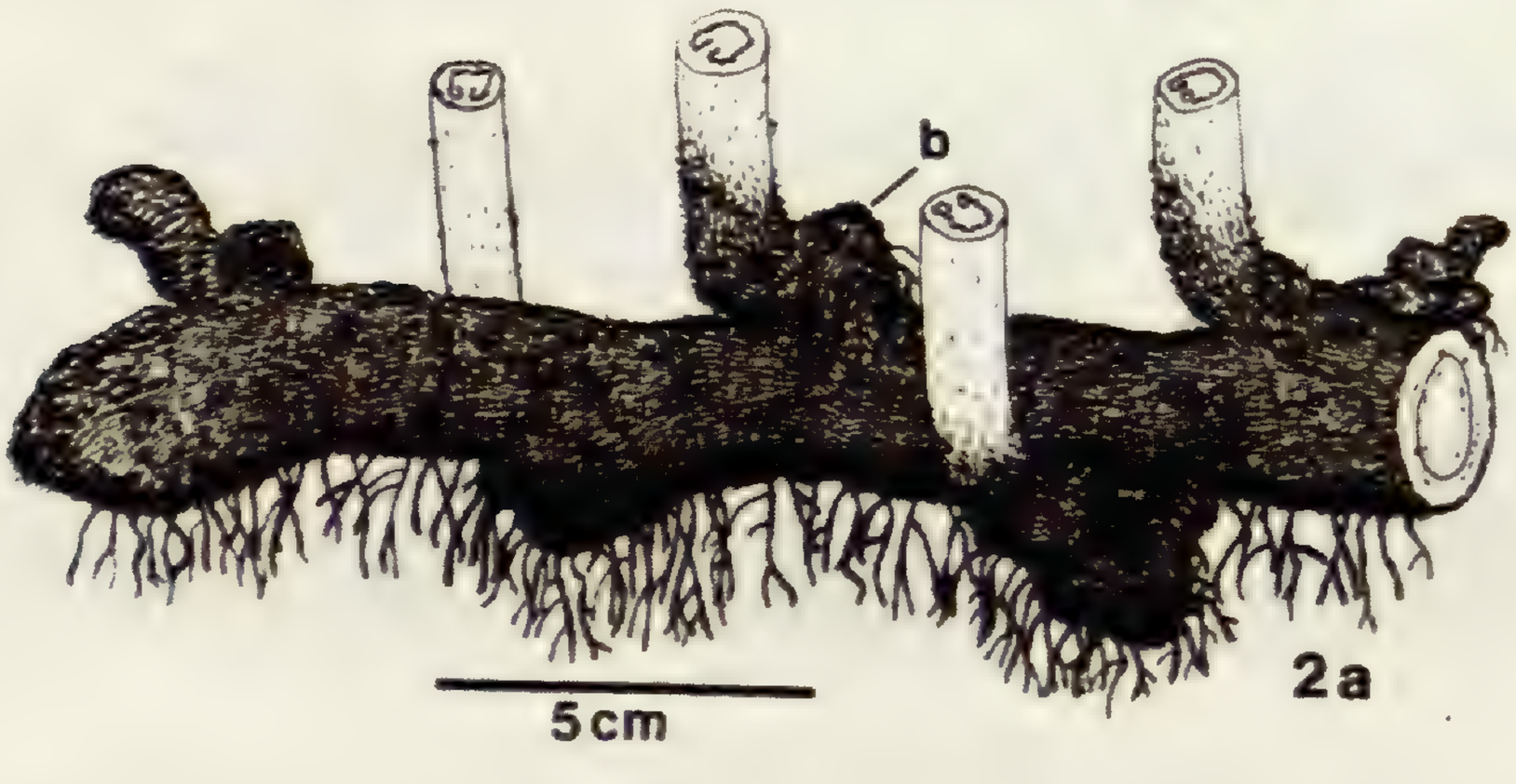
In contrast to the pattern in subg. *Culcita*, steles of subg. *Calochlaena* are circular in cross section in the long internodes and show a different pattern of lobing at the nodes (Figs. 2b, 2c). Sclerenchyma is present as islets or strands scattered throughout the cortex and pith (Fig. 4). Vascularization of branches and buds in *Calochlaena* resembles that in *Lophosoria* and *Metaxya* (Lucansky, 1974).

The configuration of the petiolar vascular bundle is very different in the two subgenera. Petiolar bundles of subg. *Culcita* have a simple form with widely diverging margins (Fig. 5; Sen, 1968) whereas those of subg. *Calochlaena* show a shallowly lobed, adaxially involute "C" shape in cross section (Fig. 6). The patterns of pinna vascularization also differ sharply in the two groups (Figs. 7, 8;

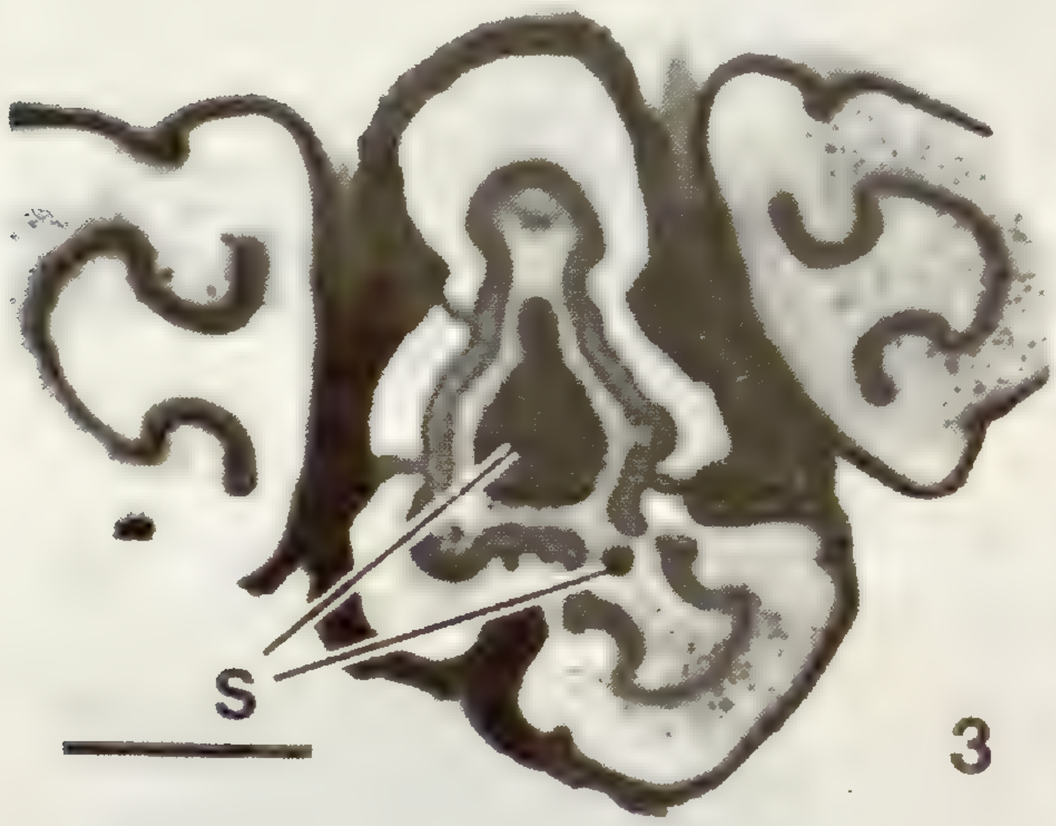








FIGS. 1–2. Shoots of *Culcita* and *Calochlaena*. FIG. 1. *Culcita coniifolia*. 1a, Erect shoot with persistent petiole bases. Apex and croziers covered with long hair, base densely clothed with roots. 1b, Cross section of mature shoot. Central stem is relatively small, most of "trunk" is composed of overlapping fleshy petiole bases, hairs and roots. FIG. 2. *Calochlaena villosa*. 2a, Creeping rhizome, branching from buds (b) on abaxial side of leaf bases. 2b, Cross section of internode. Stem is solenostelic with islets of sclerenchyma in cortex and pith. 2c, Section at node. Branch trace (bt) departing from abaxial side of leaf trace.



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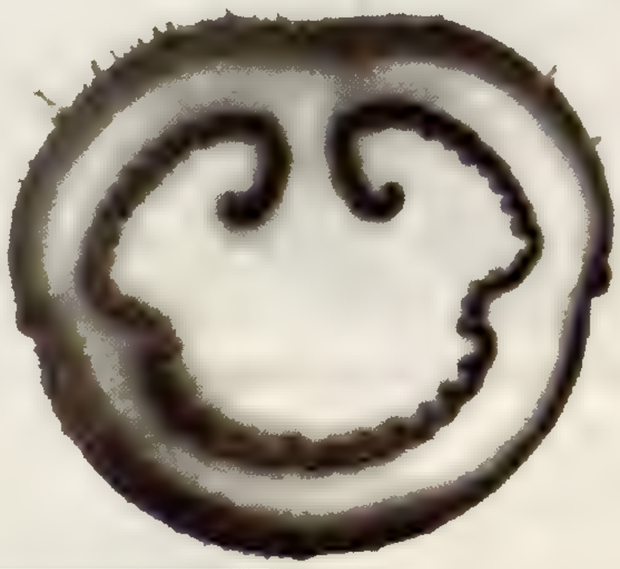

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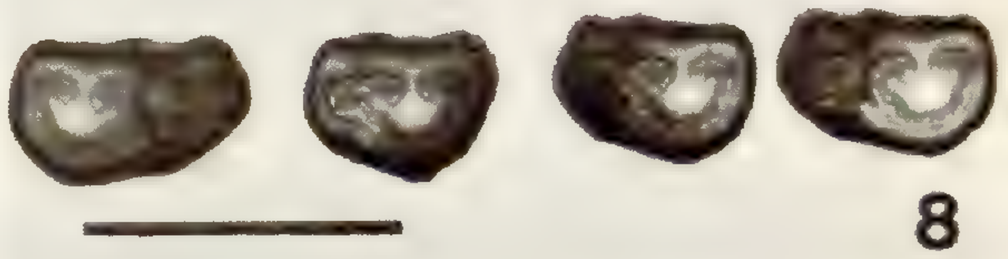

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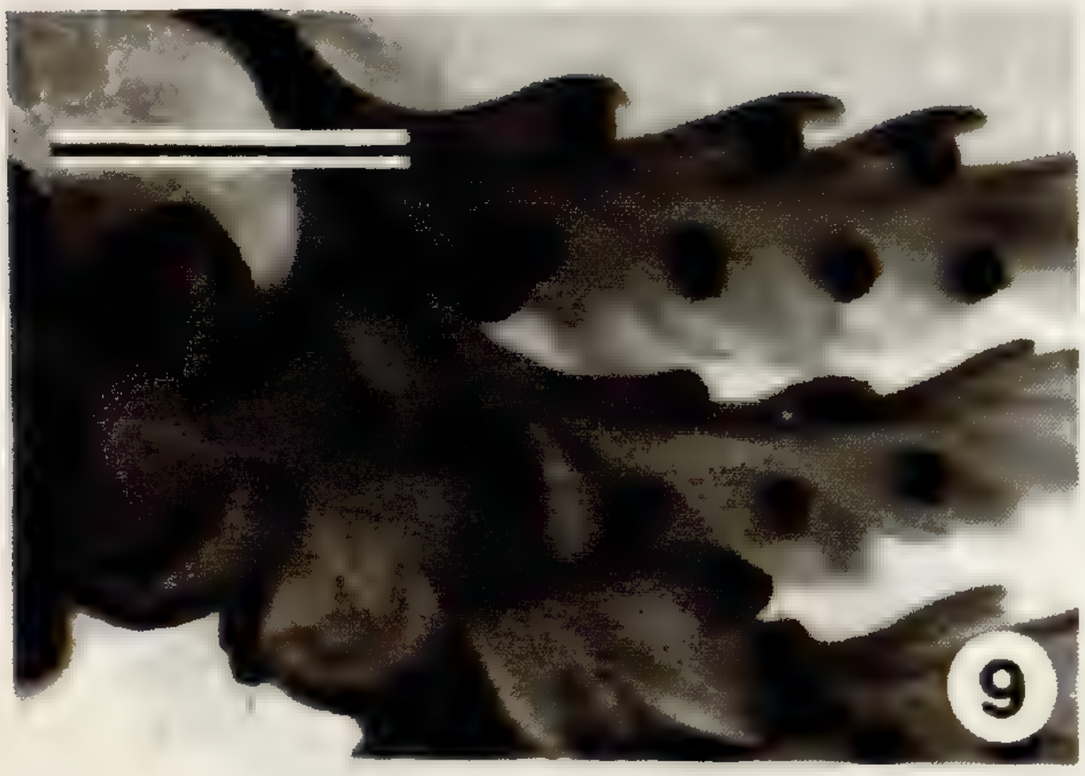
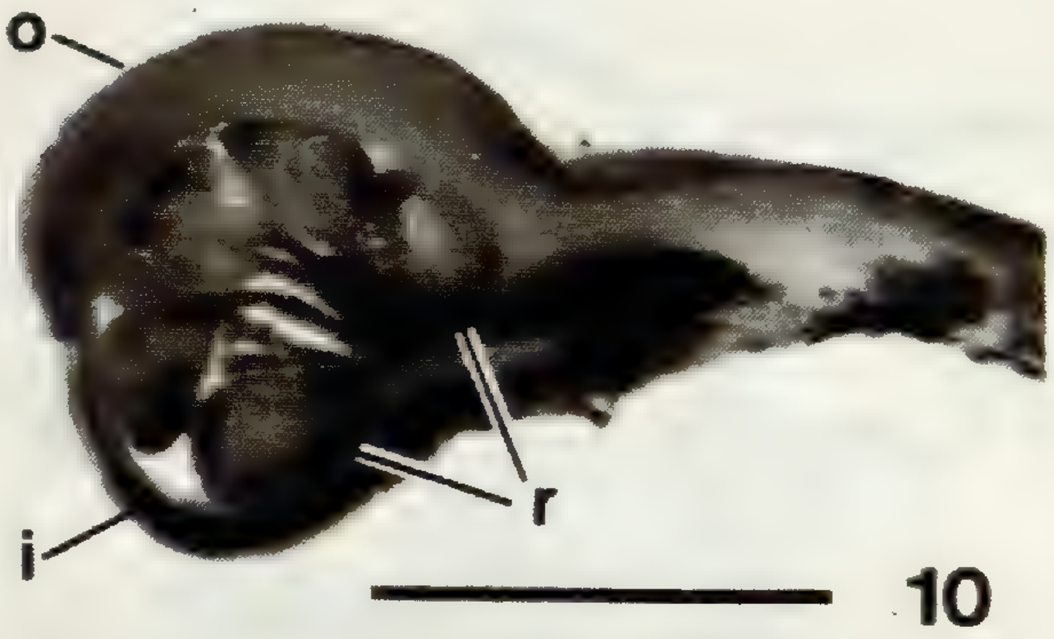
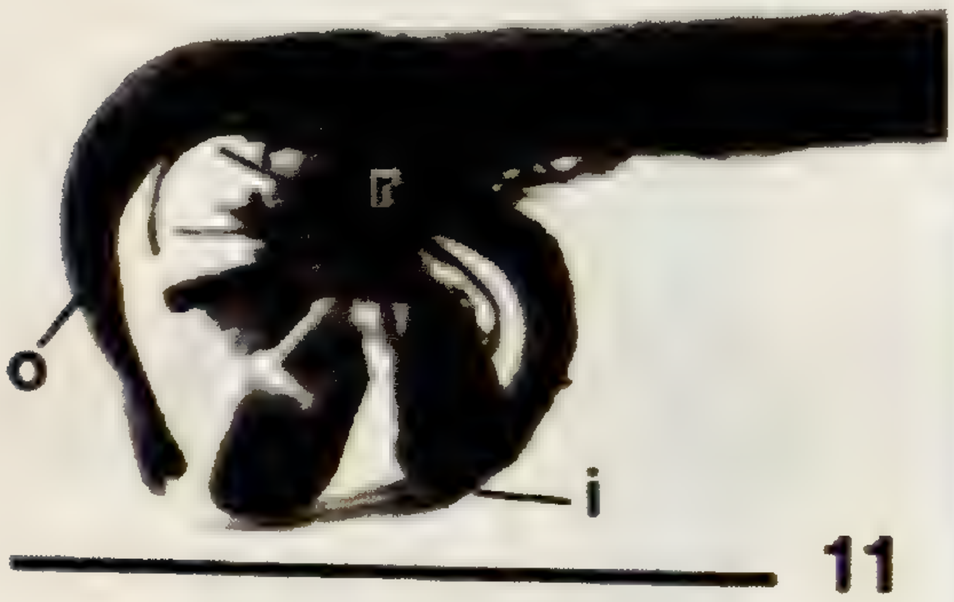
FIGS. 3–8. Anatomy of *Culcita* and *Calochlaena*. FIG. 3. *Culcita coniifolia*. Cross section of stem showing lobed solenostele. Core of sclerenchyma (s) in pith gives rise to "sclerenchyma traces." FIG. 4. Section of stem of *Calochlaena villosa*. Stem solenostelic with scattered islets of sclerenchyma in cortex and pith. FIG. 5. Cross section of petiole of *Culcita coniifolia*. Vascular bundle with diverging adaxial margins. FIG. 6. Cross section of petiole of *Calochlaena straminea*. Vascular bundle adaxially involute, corrugated. FIG. 7. Sequential sections (distal on right) of rachis of *C. coniifolia*. Pinna trace arises from margin of foliar bundle. FIG. 8. Sections of rachis of *Calochlaena villosa*. An extramarginal sector of the vascular bundle becomes the pinna trace. Scale bars = 1 cm.

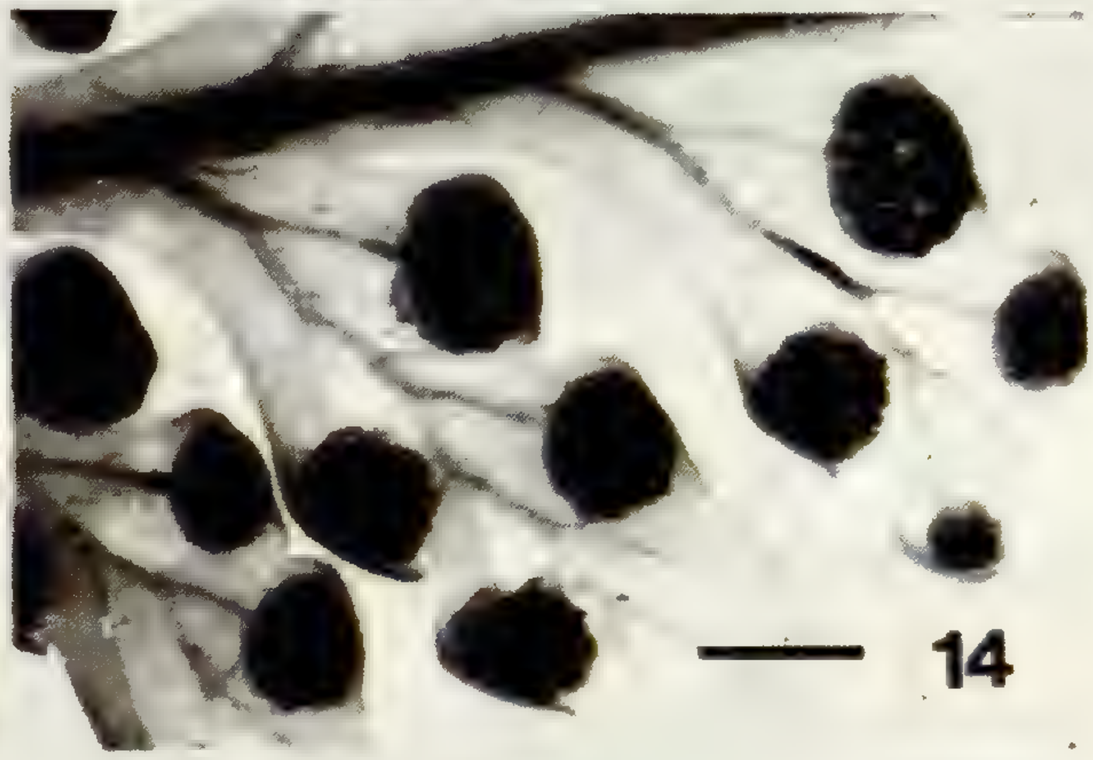
Davie, 1918). In subg. *Culcita*, pinna traces depart from the margins of the foliar bundle (Fig. 7), whereas in *Calochlaena* a wide extramarginal sector becomes the pinna trace (Fig. 8).

Prominent mucilage ducts occur in the vascular bundles of petioles and rachises of subg. *Calochlaena* but are not found in subg. *Culcita*. They are essentially identical to structures found in *Cibotium*, *Lophosoria*, and *Cyathea*. In contrast, mucilage cells occur throughout the ground tissue of *Culcita coniifolia*; these are not seen in subg. *Calochlaena*.









FIGS. 9–14. Soral morphology of *Culcita* and *Calochlaena*. FIG. 9. Large sori of *Culcita coniifolia* (on left) with those of *Calochlaena villosa*. FIG. 10. *Culcita coniifolia*. Longitudinal section of sorus. Expanded receptacle is united with base of inner indusium. Sporangia are long-stalked. FIG. 11. Section of sorus of *Calochlaena straminea* [Franc 477 (US)], showing lack of fusion of receptacle and indusium. Sporangia are short-stalked. FIG. 12. Abaxial view of sori of *Calochlaena straminea* [Setchell 389 (US)]. Sori covered by bivalved indusia. FIG. 13. Sori of *Calochlaena dubia* (US 25078). Outer indusium represented by a lobe of the margin, sorus appears inframarginal. FIG. 14. *Calochlaena dubia* [Camfield s.n. (MICH)]. Mature sori with most sporangia not covered by indusia. o = outer indusium; i = inner indusium; r = receptacle. Scale bar in Fig. 9 = 5 mm; scale bars in Figs. 10–14 = 1 mm.

Sori.—*Culcita macrocarpa* and *C. coniifolia* have large bivalved sori (Figs. 9, 10) in which the receptacle is united with base of the inner (abaxial) indusium (Tryon & Tryon, 1982). The vascular bundle of the sorus extends into the expanded receptacle (Fig. 10). The sori of *Culcita* resemble those of *Dicksonia*

which show a similar but more extensive fusion of the receptacle and indusium (Goebel, 1905; Tryon & Tryon, 1982; Churchill, 1983). Members of subg. *Calochlaena* have much smaller sori that exhibit no such fusion of the receptacle and the indusium (Figs. 9, 11). In this regard, subg. *Calochlaena* resembles *Cibotium* (see Tryon & Tryon, 1982) rather than *Dicksonia*.

There is a striking diversity of soral morphology within *Calochlaena*. Most, including *C. javanica* and *C. straminea*, have typically dicksoniaceous bivalved sori (Figs. 11, 12). The sorus of *C. dubia*, on the other hand, differs sharply from those of other dicksonioid ferns. The "outer indusium" is represented only by a slightly reflexed but unmodified lobe of the lamina so that the sorus appears to be superficial and inframarginal with a single indusial flap (Fig. 13). This characteristic formed the original basis of Maxon's subg. *Calochlaena*. Collections of *C. dubia* often have sori intermediate between this condition and that of the other members of the group.

The inner indusium encloses the maturing sporangia in *C. straminea* (Fig. 11, 12), but the sporangia of other species of *Calochlaena* are often largely exposed (Fig. 14). The inner indusium tends to be lobed or laciniate and commonly has cilia or marginal hairs. Inner indusia of some collections of *C. javanica* have trichomes and emergences on their outer surfaces.

Other differences between the subgenera have been noted in the literature. Reported chromosome numbers of $n = 66$-68 in *Culcita macrocarpa* (Manton, 1958) and $n = 66$ in *C. coniifolia* (Gómez–Pignataro, 1971) are widely different from the count of ca. 55–58 for *C. dubia* (Manton, cited by Holttum, 1963). Gastony (1981) pointed out that the two subgenera are strikingly different in spore morphology. Spores of subg. *Culcita* possess a perine, lacking in *Calochlaena*, and the psilate to microverrucate exine of subg. *Culcita* differs strongly from the sculptured exine of broad spinules found in subg. *Calochlaena*.

The two subgenera of *Culcita* appear to be united chiefly by a general resemblance in frond form and dissection and similar patterns of channelling of the upper sides of leaf axes. Apart from these probably superficial similarities, the subgenera share few or no characteristics beyond those common to other genera of dicksonioid ferns. In fact, *Calochlaena* and *Culcita* are as distinct morphologically as any two genera of dicksonioid ferns, and it is likely that each is more closely related to other genera of the group than it is to the other subgenus. The numerous differences strongly support the conclusion that subg. *Calochlaena* should be elevated to generic rank.

Calochlaena (Maxon) M. D. Turner & R. A. White, stat. nov.—*Culcita* subg. *Calochlaena* Maxon, J. Wash. Acad. Sci. 12:458–459. 1922.—TYPE: *Culcita dubia* (R. Br.) Maxon

Large terrestrial ferns. *Rhizomes* prostrate to suberect, not arborescent, often spreading by stout stolonlike branches, stem apices densely hairy with bristly or soft hairs, stems solenostelic with islets or strands of sclerenchyma in cortex and pith. *Fronds* spirally arranged, large (to 2 m or more), long-petiolate; petiolar vascular bundle simple, incurved adaxially, with vascular mucilage ducts,

pinna traces extra-marginal. Leaf axes and lamina pilose to glabrescent. Lamina deltoid, 3–4 pinnate-pinnatifid, dissection anadromous, basal pinnae largest; leaf axes adaxially grooved with grooves of large and small axes confluent; ultimate segments oblique, larger on acroscopic side, pinnatifid to toothed, venation simple. *Sori* marginal, terminal on veins on monomorphic leaves, indusia bivalved, outer indusium cuplike or (in *C. dubia*) only slightly differentiated from the lamina and sorus appearing inframarginal; inner indusium membranous, enclosing or only partly covering the sporangia, often lobed or laciniate, often marginally ciliate, sometimes with hairs on outer surface; receptacle not united with base of inner indusium; paraphyses many, on receptacle and sporangial stalks, filamentous, contorted, and vermiform. Sporangia short-stalked, annuli oblique; spores tetrahedral-trilete with broad spinules or tubercles laterally fused into ridges.

Copeland (1947) commented that the species of *Calochlaena* are "too similar", and Holttum (1963) placed two species in synonymy under *Culcita javanica*. The species listed below show consistent differences in some characters, although there appears to be much variation within species. Future systematic studies may alter these species concepts. We exclude *Culcita formosae* (Christ) Maxon (*Dennstaedtia formosae* Christ) from *Calochlaena*. It is a *Dennstaedtia*, apparently *D. smithii* (Hook.) Moore.

1. **Calochlaena dubia** (R. Br.) M. D. Turner & R. A. White, comb. nov.—*Davallia dubia* R. Br., Prodr. 157. 1810—*Dicksonia dubia* (R. Br.) Gaudich., Voy. Bonite, Bot. 367. 1827.—*Sitolobium dubium* (R. Br.) Brackenr., U. S. Expl. exped., Filic. 16:273. 1854.—*Balantium dubium* (R. Br.) Copel., Philipp. J. Sci. 3:301. 1908—*Culcita dubia* (R. Br.) Maxon, J. Wash. Acad. Sci. 12:458. 1922.

Balantium brownianum C. Presl, Tent. pterid. 134. 1836.

Hemitelia godeffroyi Luerssen, J. Mus. Godeffroy. 3:4. 1873. (*fide* D. B. Lellinger, in litt.).—TYPE: Australia, Brisbane River, *Dietrich 26*.

Culcita blepharodes Maxon, J. Wash. Acad. Sci. *12*: 459. 1922.—TYPE: Fiji, Lomo-Lomo, *Wilkes Expedition* (US!).

Range:—Eastern Australia.

The type of *Culcita blepharodes* closely agrees with several Australian collections of the variable *C. dubia*. Possibly this specimen was incorrectly attributed to Fiji, or it may represent a waif or temporary introduction. We have seen no other Fijian specimens of this species, and it is omitted from Brownlie's (1977) flora.

2. **Calochlaena straminea** (Labill.) M. D. Turner & R. A. White, comb. nov.—*Dicksonia straminea* Labill., Sert. austro.–caledon. 7., pl. 10. 1824.—*Dennstaedtia straminea* (Labill.) J. Smith, Hist. fil. 265. 1875.—*Balantium stramineum* (Labill.) Diels in Engl. & Prantl, Nat. Pflanzenfam. 1(4):119. 1899. (not *Sitolobium stramineum* Brackenr.).—TYPE: New Caledonia, *Labillardière s.n.* (P).

Dicksonia torreyana Brackenr., U. S. Expl. exped., Filic. 16. 278, pl. 38, f. 2. 1854.

Range:—New Caledonia, Fiji, Samoa, Vanuatu (New Hebrides), Solomon Islands, Admiralty Islands, New Guinea, SE Philippines.

3. **Calochlaena javanica** (Blume) M. D. Turner & R. A. White, comb. nov.—*Dicksonia javanica* Blume, Enum. pl. Javae. 240. 1828.—*Dennstaedtia javanica* (Blume) Christ, Bull. Herb. Boissier, sér. II. 4:617. 1904.—*Balantium javanicum* (Blume) Copel., Philipp. J. Sci. 4:62. 1909.—*Culcita javanica* (Blume) Maxon, J. Wash. Acad. Sci. 12:456. 1922—TYPE: Java, *Blume s.n.* (L; isotype US!).

Dicksonia copelandii Christ, Philipp. J. Sci., Bot. 2:183. 1907.—*Balantium copelandii* (Christ) Christ, in Copel., Philipp. J. Sci. 3:301. 1908.—*Culcita copelandii* (Christ) Maxon, J. Wash. Acad. Sci. 12:457. 1922.—SYNTYPES: Philippines, Luzon, Baguio, Benguet Province, 1400 m, *Loher s.n.*; Baguio, Benguet Province, *Elmer 6025*; Bagnen, Lepanto District, 2000 m, *Copeland 1912*.

Balantium pilosum Copel., J. Straits Branch Roy. Asiat. Soc. 63:71–72. 1912.—*Culcita pilosa* (Copel.) C. Chr., Index fil. suppl. 3. 57. 1934.—TYPE: Borneo, Bukit Lawi, Ulu Limbang.

Range:—Java, Borneo, Philippine Islands.

We follow Holttum (1963) in including in *C. javanica* the plants from Borneo and the Philippines that have been called *Culcita copelandii*. *Calochlaena javanica* and *C. villosa* appear to be closely related. They may eventually prove to be a single widespread and variable species.

4. **Calochlaena villosa** (C. Chr.) M. D. Turner & R. A. White, comb. nov.—*Culcita villosa* C. Chr., Brittonia 2:283. 1937.—TYPE: New Guinea, Urunu, Vanapa Valley, 1900 m, *Brass 4791* (BM; isotypes US!, GH!).

Range:—New Guinea.

Christensen noted the small inner valve of the indusium in *C. villosa* and suggested it might be placed with *C. dubia* in Maxon's subg. *Calochlaena*. This species is close to *C. javanica*. Holttum (1964) erroneously labeled this species "pilosa" on a distribution map (Gastony, 1981).

5. **Calochlaena novae–guineae** (Rosenstock) M. D. Turner & R. A. White, comb. nov.—*Davallia novae-guineae* Rosenstock, Repert. Spec. Nov. Regni. Veg. 5:36. 1908.—*Leptolepia novae-guineae* (Rosenstock) Alderw., Malayan ferns 283. 1909.—*Ithycaulon novae-guineae* (Rosenstock) Alston, J. Bot. 77:289. 1939.—*Oenotrichia novae-guineae* (Rosenstock) Copel., Univ. Calif. Publ. Bot. 16:82. 1929.—TYPE: New Guinea, Mt. Gelu, 1700 m, *Werner* (isotype US!).

Range:—New Guinea.

This distinctive species has long been wrongly placed in the genus *Oenotrichia* (Dennstaedtiaceae). *Calochlaena novae-guineae* is distinguished

from *C. villosa* by its larger, more coarsely divided leaves with pinnae diverging at a wide angle, larger sori and sporangia, and larger, differently sculptured spores. Few collections have been seen: *Millar & Holttum N. G. F. 15835*, near Wau, Morolee dist., Bulldog Rd., Edie Creek, 6,900 ft.; *Marchant 78.363*, Wau, forming dense thickets on summit of Mt. Kindie.

Relationships of *Calochlaena*

Culcita (including *Calochlaena*) has been assigned several different systematic positions by different authors. It was put in subfamily Dicksonieae of the Cyatheaceae with *Dicksonia* and *Cibotium* by Diels (1899). Bower (1926) and Christensen (1938) similarly classified it in the Dicksonieae of the Dicksoniaceae. Copeland (1947) included all dicksonioid genera in a large, heterogeneous family Pteridaceae. Holttum and Sen (1961) assigned *Culcita* to subfamily Thyrsopteridoideae of the Cyatheaceae. Other workers have placed *Culcita* with *Thyrsopteris* and *Cibotium* in a separate family Thyrsopteridaceae (Mabberley, 1987). *Culcita* was put in a separate family Culcitaceae by Pichi Sermolli (1977). Although it is debatable which familial scheme best expresses the phylogenetic relationships of the plants, it is clear to us that *Calochlaena* should not be placed with *Culcita* in a separate family or subfamily. Even though detailed phylogenetic analyses of the dicksonioid ferns are lacking, *Calochlaena* is evidently only remotely related to *Culcita*. Both genera seem isolated among the tree ferns, but *Calochlaena* is more similar to *Cibotium* and even *Lophosoria* than it is to *Culcita*. *Culcita* stands apart from the other genera in shoot anatomy and morphology, but the similar fusion of receptacle and lower indusium indicates a possible relationship with *Dicksonia*. Spore characteristics also suggest a link between *Culcita* and *Dicksonia* (Gastony, 1981). Anatomically, neither *Calochlaena* nor *Culcita* show any close affinity with *Thyrsopteris*.

It has been suggested that *Culcita/Calochlaena* is an evolutionary link between the dicksonioid ferns and *Dennstaedtia* (e.g., Copeland, 1908, 1909, 1947; Christensen, 1938), and the genus is included in the Dennstaedtiaceae by Duncan and Isaac (1986). We believe that the strong superficial resemblance of *Calochlaena* to some Dennstaedtiaceae does not reflect a close phylogenetic relationship. In important details of shoot anatomy and morphology, *Calochlaena* resembles other dicksonioid ferns and differs from *Dennstaedtia*.

As noted above, several authors have at various times noted that differences between *Culcita* and *Calochlaena* suggest that they could be separate genera. The addition of evidence from shoot anatomy has made it clear that the two groups are as dissimilar as any two genera of dicksonioid ferns. The recognition that *Culcita* and *Calochlaena* are two distinct genera will affect any future discussions of the systematics, biogeography, and evolution of the tree ferns.

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Literature Cited

Bower, F. O. 1926. *The ferns*. Vol. II. London: Cambridge University Press.

Brownlie, G. 1977. The pteridophyte flora of Fiji. Vaduz: J. Cramer.

Christensen, C. 1938. Filicinae. Pp. 522–550 in *Manual of pteridology*, ed. F. Verdoorn. The Hague: Nijhoff.

Churchill, H. W. 1983. Comparative developmental studies of the leaf and sorus of tree ferns. Ph.D. dissertation, University of Massachusetts.

Copeland, E.B. 1908. Fern genera new to the Philippines. Philipp. J. Sci. 3:301–302.

———. 1909. Ferns of the Malay–Asiatic region. Philipp. J. Sci. 4:1–65.

———. 1947. *Genera filicum*. Waltham, Massachusetts: Chronica Botanica.

Davie, R.C. 1918. A comparative list of fern pinna-traces, with some notes on the leaf-trace in the ferns. Ann. Bot. (London) 32: 233–245.

Diels, F. 1899. Cyatheaceae. Pp. 113–139 in *Die Natürlichen Pflanzenfamilien*, Teil I, Abt. 4., ed. A. Engler and K. Prantl. Leipzig.

Duncan, B.D. and G. Isaac. 1986. *Ferns and allied plants of Victoria, Tasmania and South Australia*. Carlton, Victoria: Melbourne Univ. Press.

Fraser–Jenkins, C. R., and M. Laínz. 1983. *Culcita macrocarpa*—a new locality in Spain. Fern Gaz. 12:299–301.

Gastony, G. 1981. Spore morphology in the Dicksoniaceae. I. The genera *Cystodium*, *Thyrsopteris*, and *Culcita*. Amer. J. Bot. 68:808–819.

Goebel, K. 1905. *Organography of plants*. II. *Special organography*. trans. ed. by I.B. Balfour. Oxford: Clarendon Press.

Gómez–Pignataro, L.D. 1971.Ricerche citologiche sulle pteridofite della Costa Rica. 1. Ist. Bot. Reale Univ. Reale Lab. Crittog. Pavia Atti ser. 6. 7:29–31.

Holttum, R.E. 1963. Cyatheaceae. Flora Malesiana Ser. II, 1: 65–176.

———. 1964. Distribution of some of the more primitive ferns of Mt. Kinabalu. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 161:38–48.

——— and U. Sen. 1961. Morphology and classification of the tree ferns. Phytomorphology 11:406–420.

Lucansky, T.W. 1974. Comparative studies of the nodal and vascular anatomy in the neotropical Cyatheaceae. *I. Metaxya* and *Lophosoria*. Amer. J. Bot. 61:464–471.

Mabberley, D.J. 1987. *The plant book*. Cambridge: Cambridge University Press.

Manton, I. 1958. Chromosomes and fern phylogeny with special reference to "Pteridaceae". J. Linn. Soc., Bot. 56:73–91.

Maxon, W.R. 1922. The genus *Culcita*. J. Wash. Acad. Sci. 12: 454–460.

Pichi Sermolli, R.E.G. 1977. Tentamen pteridophytorum genera in taxonomicum ordinem redigendi. Webbia 31:313–512.

Roy, S.K., and R.E. Holttum. 1965. New cytological records for *Cystodium* and *Dicksonia*. Amer. Fern. J. 55:35–37.

Schmid, R. and M.D. Turner. 1977. Contrad 70, an effective softener of herbarium material for anatomical study. Taxon 26:551–552.

Sen, U. 1968. Anatomy of *Culcita macrocarpa*. Canad. J. Bot. 46:43–46.

Tryon, R. and A. Tryon. 1982. *Ferns and allied plants with special reference to tropical America*. New York: Springer–Verlag.

White, R.A. 1984. Comparative development of vascular tissue patterns. Pp. 53–107 in *Contemporary problems in plant anatomy*, ed. R.A. White and W.C. Dickison. New York: Academic Press.

Zimmerman, M.H. and P.B. Tomlinson. 1965. Anatomy of the palm *Rhapis excelsa*. I. Mature vegetative axis. J. Arnold Arbor. 46:160–177.

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The Significance of Spore Banks in Natural Populations of *Athyrium pycnocarpon* and *A. thelypterioides*

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How do homosporous plants survive in variable environments? One mechanism available to plants is seed or spore dormancy (Cohen 1966, 1967). An observable consequence of seed and spore dormancy is the formation of a seed or spore bank (Harper, 1977; Grime, 1979). Work in this area goes back at least to Darwin (1859), who assayed a cupful of mud from a stream bank for viable seeds.

Cohen (1966, 1967, 1968) developed models of seed and spore dormancy describing the environmental conditions favoring its evolution. He predicted that dormancy will evolve when the variance of environmental quality greatly exceeds the mean of environmental quality. Under this condition natural selection will favor individual seeds and spores that a) have delayed germination and prolonged viability, as a means of avoiding unfavorable environmental conditions, and b) germinate only in response to those environmental signals that correlate positively with future success. These models have served as a basis for a number of publications discussing the effects of seed dormancy on the distribution and abundance of seed plants (Leon, 1985; Brown & Venable, 1986; Ellner, 1985a,b). To understand the effect of spore dormancy on fern ecology, knowledge of spore characteristics and of the benefits and consequences of delayed spore germination is needed.

There are many in vitro studies of the physiological characteristics associated with spore dormancy. Prolonged viability has been reported for a wide variety of fern taxa (Lloyd & Klekowski, 1970). Differential response to germination cues is well known, particularly light quality (Towill & Ikuma, 1973; Mohr, 1956; Sugai & Furuya, 1967; Tomizawa et al., 1983), light quantity (Isikawa & Oohusa, 1956; Eakle, 1975) and hormones (Schraudolf, 1985; Howland & Edwards, 1979). There is little information of spore banks among natural populations of ferns, although Leck and Simpson (1987) provided evidence of spore banks among naturally occurring pteridophyte populations. In order to expand our knowledge of spore banks, I assayed soils from among populations of *Athyrium pycnocarpon* (Sprengel) Tidestrom and *Athyrium thelypterioides* (Michx.) Desv. for dormant spores.

MATERIALS AND METHODS

Soil samples were collected from natural populations of *Athyrium pycnocarpon* and *Athyrium thelypterioides* in Hawk Woods, an oak dominated

woods in the city of Athens, Ohio (T9N R14W Athens, Ohio quadrangle: 82° 4′ 30″ W, 39° 21′ 30″ N), and from Long Run, a beech/maple woods within Wayne National Forest near Glouster, Ohio (T11N R14W sec. 11 Corning, Ohio quadrange: 82° 4′ 30″ W, 39° 32′ 30″ N).

Other pteridophytes at the Hawk Woods site were *Thelypteris noveboracensis*, *Adiantum pedatum*, and *Polystichum acrostichoides*. These species were also present at the Long Run site, along with *Dryopteris goldiana*, *Cystopteris fragilis*, and *Thelypteris hexagonoptera*.

To ascertain whether storage of soil under refrigeration influenced spore assay results, samples from the top 1 cm of the soil were collected on 26 October 1986, from populations of *Athyrium thelypterioides* and of *Athyrium pycnocarpon* in Hawk Woods and stored in a refrigerator at 4° C. Each month, from November 1986 to April 1987, five 2–gram aliquots were removed from each sample and inoculated onto 15 mm petri dishes filled with a nutrient agar medium prepared as described by Klekowski (1969). The soil was spread evenly across the surface of the agar, forming a thin layer. The inoculated petri dishes were then incubated for 30–40 days under continuous incandescent and fluorescent light totalling approximately 30 $\mu E/m^2 sec$, at room temperature. Each dish was then assayed for the total number of gametophytes present. The results of this assay were used as an estimate of the number of viable spores present in the soil. Similar samples were again collected from the same populations in April 1987, with five 2-gram aliquots assayed as described above. The month of April was chosen to compare the effects of overwintering in the soil to storage during that time in a refrigerator. None of the above-mentioned locally occurring taxa were observed to release spores during the winter or early spring, although a systematic study of that specific feature was not undertaken. A final assay of the soil collected in October 1986 was completed in January of 1988, specifically to determine spore viability. Data were analyzed using the completely randomized design analysis of variance (CRD), and means compared using the least significant difference parameter (LSD), as described by Steel and Torrie (1980).

Nine vertical soil cores were collected from populations of both species from Long Run between June 1987 and January 1988, and assayed for the presence of viable spores as described above. An 18 inch soil sampling tube with $^{13}/_{16}$ inch inside diameter was used to collect soil cores. Due to compaction, this corer could only be used to sample the soil to a depth of 16 cm. The number of spores per gram of soil at each centimenter of depth in each core was estimated using the method described above.

Assuming the density of the soil to be 1 gram per cm^3, an underestimate (Hausenbuiller, 1978), and given that there are 10,000 cm^3 in a volume 1 m × 1 m × 1 cm, the estimated number of spores in a "slice" of the soil column 1 m × 1 m × 1 cm, for each cm of soil depth, was the number of spores per gram in the sample from that depth × 10,000. The values at all levels were then summed to give an estimate of the number of spores in the volume of soil beneath each square meter of the soil surface. The mean number of spores at each level was also estimated, along with the mean number of spores beneath each square meter of soil surface. This underestimates the number of spores per square meter due

to the above assumptions and because the entire spore-containing column was not assayed where the soil was deeper than 16 cm.

Following the assay for spores, gametophytes from each culture were transferred to soil pots. Fertilization was promoted by regularly flooding the surface of each pot. The resulting sporophytes were used to determine the species composition at each level.

Results

Ungerminated *Athyrium pycnocarpon* and *A. thelypterioides* spores were found to be present in the soil at both sites. *Polystichum acrostichoides* and *Thelypteris noveboracensis* were also present in the soil at the Hawk Woods site. Only the *Athyrium* species and *Adiantum pedatum* were identifiable in cultures of soil collected at the Long Run site, as the sporophyte cultures died before identification of other species could be made. These species were present throughout the soil column.

There were significant differences among months for the number of spores germinating from soil stored under refrigeration ($p < .001$ for *A. pycnocarpon* $p < 0.025$ for *A. thelypteroides*). Comparison of means (Tables 1, 2) revealed that for both species, germination increased significantly following one month of storage under refrigeration, then dropped significantly by the 5th month of storage. For *A. pycnocarpon*, there was a significant increase in germination from the fifth to the sixth month of storage. There was no such increase for *A. thelypterioides*. Germination for month 5 was significantly lower than germination for month 1 in both species; however, month 6 was not significantly different from month 1. There was no difference in germination between month 1 and the sample collected in April 1987 in both species, but significantly more

Table 1. Mean Number of Spores Germinating in 2 Grams of Soil from an *Athyrium pycnocarpon* Population. Nov 86 to Apr 87 and Feb 88 are results from soil collected in October 1986. Apr 87A is the result from soil collected in April 1987. Data in matrix are differences among means. Lower case characters indicate that the difference between means compared is significant: a, $p < 0.05$; b, $p < 0.01$; c, $p < 0.001$.

Nov 86	Dec 86	Jan 87	Feb 87	Mar 87	Apr 87	Apr 87A	Feb 88
336.6	519.8	308.0	274.8	178.0	299.8	255.0	302.4

	Feb 88	Apr 87A	Apr 87	Mar 87	Feb 87	Jan 87	Dec 86
Nov 86	34.2	81.6	36.8	158.6[c]	61.8	28.6	182.3[c]
Dec 86	217.4[c]	264.8[c]	220.0[c]	341.8[c]	245.0[c]	211.8[c]	
Jan 87	5.6	53.0	8.2	130.0[b]	33.2		
Feb 87	27.6	19.8	25.0	96.8[a]			
Mar 87	124.4[b]	77.0	121.8[c]				
Apr 87	2.6	44.8					
Apr 87A	47.4						

TABLE 2. Mean Number of Spores Germinating in 2 Grams of Soil from an *Athyrium thelypterioides* Population. Nov 86 to Apr 87 and Feb 88 are results from soil collected in October 1986. Apr 87A is the result from soil collected in April 1987. Data in matrix are differences among means. Lower case characters indicate that the difference between means compared is significant: a, $p < 0.05$; b, $p < 0.02$; c, $p < 0.01$; d, $p < 0.001$.

Nov 86	Dec 86	Jan 87	Feb 87	Mar 87	Apr 87	Apr 87A	Feb 88
98.4	140.6	126.4	95.4	62.2	79.2	127.4	86.8

	Feb 88	Apr 87A	Apr 87	Mar 87	Feb 87	Jan 87	Dec 86
Nov 86	11.6	29.0	19.2	36.2[a]	3.0	28.0	42.2[b]
Dec 86	54.2[c]	13.2	61.4[d]	78.0[d]	45.2[c]	14.2	
Jan 87	39.6[a]	1.0	47.2[c]	64.2[d]	31.0		
Feb 87	8.6	32.0	16.2	33.2[a]			
Mar 87	24.6	65.2[d]	17.0				
Apr 87	7.6	48.2[c]					
Apr 87A	40.6[b]						

A. pycnocarpon spores germinated in the soil stored for 1 month than in soil collected in April 1987. The number of spores germinating in 15-month old cultures was the same as in fresh cultures, but was significantly fewer than in one month old cultures for both species. Basic trends in germination were the same for both species.

Soil depth at sites sampled ranged from 8 cm deep to more than 16 cm deep. Viable spores were present throughout the soil column (Table 3). A bimodal distribution is apparent, with peaks in spore numbers at the surface and at a depth of 13 cm (Table 3). While some variation existed among cores, spore numbers were consistently within the 10^6 order of magnitude beneath each square meter of the soil surface (Table 3).

DISCUSSION

Assays of spore numbers in the soil column confirm the presence of a spore bank. Spores of both *A. pycnocarpon* and *A. thelypterioides* are components of the spore bank. Schneller (1979) observed prolonged viability in *A. filix-femina*, which, along with these results, indicates that spore banks are characteristic of temperate *Athyrium* species.

Significant variation existed among months when soil was assayed for viable spores following storage in a refrigerator. The consistency in the pattern of spore germination between the two species, particularly the increases after 1 month and 6 months of storage, indicates that there may be induced dormancies in some of the spores assayed. Whatever the cause, assays of soil stored for different

TABLE 3. Estimated Numbers of Spores in Soil Sampled in Wayne National Forest. Estimates are number of spores per volume of soil 1 meter × 1 meter × 1 centimeter. Totals are numbers per square meter of the soil surface.

	Date sample collected				
Depth	11 June 87	14 June 87	16 Oct 87	16 Oct 87	16 Oct 87
1 cm	790,000	580,000	485,000	930,000	180,000
2 cm	700,000	625,000	207,000	415,000	320,000
3 cm	145,000	185,000	180,000	455,000	360,000
4 cm	350,000	380,000	390,000	485,000	430,000
5 cm	45,000	230,000	375,000	365,000	85,000
6 cm	60,000	160,000	195,000	480,000	270,000
7 cm	60,000*	40,000	140,000	255,000	125,000
8 cm	60,000	50,000	0	255,000	75,000
9 cm	180,000	30,000	80,000		155,000
10 cm	225,000	15,000	40,000		190,000
11 cm	425,000				50,000
12 cm	495,000				
13 cm	645,000				
14 cm	215,000				
15 cm	25,000				
16 cm	165,000				
total	4,585,000	2,295,000	2,002,000	3,640,000	2,224,000

* sample lost, result estimated.

	Date sample collected				
Depth	1 Jan 88	1 Jan 88	1 Jan 88	1 Jan 88	Mean at each level
1 cm	320,000	460,000	270,000	305,000	480,000
2 cm	465,000	535,000	315,000	325,000	434,111
3 cm	490,000	150,000	385,000	165,000	322,444
4 cm	670,000	250,000	205,000	275,000	381,667
5 cm	465,000	275,000	180,000	195,000	246,111
6 cm	415,000	245,000	185,000	190,000	244,444
7 cm	660,000	245,000	415,000	195,000	237,222
8 cm	230,000	170,000	405,000	75,000	146,667
9 cm	355,000	90,000	385,000	85,000	170,000
10 cm	110,000	10,000	260,000	55,000	113,125
11 cm	155,000	100,000	85,000	190,000	167,500
12 cm	115,000	60,000	160,000	85,000	183,000
13 cm	370,000	230,000	70,000	111,000	285,200
14 cm	65,000	180,000	90,000	55,000	121,000
15 cm	120,000	250,000	95,000	35,000	105,000
16 cm	35,000	100,000	120,000	20,000	88,000
total	5,040,000	3,350,000	3,625,000	2,360,000	4,275,000

lengths of time cannot be expected to yield homogenous results. Further studies may yield data indicating induced spore dormancies such as those described for seeds (Baskin & Baskin, 1988).

Results clearly show a reserve of spores in the soil. Leck and Simpson (1987) reported finding 10^3 spores of *Onoclea sensibilis* in the soil column beneath one square meter of soil in each of a scrub forest, high marsh, and cattail marsh. Since this species accounted for about 98% of the fern spores found, the total spore densities reported by Leck and Simpson are about $^1/_{1000}$ of those I have observed at the Long Run site. They also reported finding 98.8% of all fern spores in the top 2 cm of the soil column, again greatly different from my results. These differences suggest that there is significant variation in spore bank characteristics among fern taxa.

Germination strategies are expected to vary as environmental conditions vary (Cohen, 1966, 1967). Variation in natural environments occurs between two extremes. At one extreme, the environment is constant and of sufficient quality to maintain adapted populations. At the other extreme, the environment is highly variable, predominantly inhospitable to organisms but occasionally of sufficient quality for an organism to complete its life cycle. In favorable environments that are constant temporally and spatially, dormancy would not be expected. Under these conditions a delay in germination would increase the probability of spore death. In variable environments, reproductive success is correlated with environmental quality at the time of germination. The cost of dormancy (increased spore death) is offset by the benefit gained by avoiding germination in low quality environments. When the benefit of dormancy exceeds its cost, spores with capacities for dormancy will increase in frequency in a population. Models of seed dormancy predict that in many less extreme environments, a mixed strategy of both immediate and delayed germination will be most successful (Cohen, 1967; Leon, 1985; Ellner, 1985a). Investigations of natural populations have revealed such a mixed strategy. (Cavers & Harper, 1966; Baskin & Baskin, 1976; Harper, 1977).

Since seeds and spores represent different stages in the life history of vascular plants, models of seed dormancy may be inapplicable to spores. Brown and Venable (1986) suggested that models of dormancy should account for its effect on each life history stage. This consideration is necessary, since the environmental conditions suitable for one life history stage may be lethal for another. I suggest the following basic model for determining spore fitness as a function of the expected reproductive success of its phenotype. Pteridophytes produce spores, which, at the time of production, have some fitness,

$$W_s = P(g) \times P(f) \times P(m) \times n$$

where W_s is the absolute spore fitness at the time it is produced, P(g) is the probability that it will germinate, P(f) is the probability that a gamete from the resulting gametophyte will participate in a fertilization, P(m) is the probability that the resulting sporophyte will reach sexual maturity and n is the total number of spores expected from the mature sporophyte. Fitness is measured as an absolute, but it can be easily standardized to yield relative fitness.

The model presented above incorporates the response of a give phenotype at each of its life history stages. This model requires an understanding and further elaboration of the effect of dormancy on each stage of the pteridophyte life cycle. The hypothesis that spore and seed dormancy evolved in response to environmental variation is the result of studies of seed plants. Another possible role of a spore bank, discussed below, would be unique to pteridophytes.

The pattern of spore dispersal from ferns is the same as the pattern of seed dispersal from angiosperms. Following dispersal, the majority of the spores released from a frond are found within a few meters of the frond (Raynor et al., 1976). This distribution of spores is non random. The soil into which spores are dispersed is not a static medium: soil is a very dynamic living ecosystem (Adams, 1985; Hausenbuiller, 1978). Small particles within the soil, including spores, are moved about by animals. The most active animals within soils are earthworms (Darwin, 1881; Adams, 1986).

Earthworms feed by ingesting the soil within which they move. They retain this soil while they digest those materials their digestive systems are capable of processing. Earthworm excretions form characteristic structures known as casts (Lee, 1985). These casts are excreted both on the surface of and within the soil matrix. The net effect of earthworm activity has been studied by observing the occurrence of worm casts.

Lee (1985) summarized investigations that suggest that from 50% to almost 100% of the aggregates found in the top few centimeters of the soil are earthworm casts. Lee calculated that 25% of the A_h soil horizon passes through earthworm guts yearly in a temperate pasture. As Darwin (1881) suggested, there is a large cumulative effect of earthworm activity. Vimmerstedt (1983) observed that in 174 days, surface litter moved down into the soil to an average depth of 5.5 cm when earthworms were present, but only to 10 mm in soil without earthworms. The net effect of earthworm activity is a 55 × increase in the downward rate of movement of litter. This movement of soil is critical to any dormant spore, as failure to germinate immediately will probably result in its burial by earthworms. Earthworm activity also allows for a probability of future reemergence on the soil surface. Earthworms, as agents of spore burial and spore reemergence, become a significant ecological factor in pteridophyte populations.

Earthworms move horizontally as well as vertically. Unbiased movement of earthworms with respect to direction would result in the diffusion of spores within the soil matrix. Such diffusion of spores could potentially have a large effect on pteridophyte reproductive ecology. The effect of soil diffusion depends on a number of factors: 1) the rate of diffusion; 2) the length of time ungerminated spores remain viable; and 3) the length of time between spore dispersal and spore germination. Spore viability and germination characteristics are partly a function of the characteristics of the spore. Rate of diffusion is entirely a function of the soil environment. Variation of these factors could affect the probability of outcrossing in gametophyte populations. Study of the effects of spore randomization on pteridophyte reproductive strategies are needed to increase our understanding of how pteridophyte breeding systems are regulated.

Literature Cited

Adams, J. A. 1986. *Dirt*. College Station: Texas A & M University Press.

Baskin, C. C. and J. M. Baskin. 1988. Germination ecophysiology of herbaceous plant species in a temperate region. Amer. J. bot. 75: 286–305.

Baskin, J. M. and C. C. Baskin. 1976. Germination dimorphism in *Heterotheca subaxillaris* var. *subaxillaris*. Bull. Torrey Bot. Club. 103:201–206.

Brown, J. and D. L. Venable. 1986. Evolutionary ecology of seed-bank annuals in temporally varying environments. Amer. Naturalist 127:31–47.

Cavers, P. B. and J. L. Harper. 1966. Germination polymorphism in *Rumex crispus* and *Rumex obtusifolius*. J. Ecol. 54:367–382.

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. J. Theor. Biol. 12:119–129.

———. 1967. Optimizing reproduction in a randomly varying environment when a correlation may exist between conditions at the time a choice has to be made and the subsequent outcome. J. Theor. Biol. 16:1–14.

———. 1968. A general model of optimal reproduction in a randomly varying environment. J. Ecol. 56:219–228.

Darwin, C. 1859. *The origin of species*. London: John Murray.

———. 1881. *The formation of vegetable mould through the action of worms*. London: John Murray.

Eakle, T. W. 1975. Photoperiodic control of spore germination of *Acrosticum aureum*. Amer. Fern J. 65:94–95.

Ellner, S. 1985a. ESS germination strategies in randomly varying environments. I. Logistic-type models. Theor. Pop. Biol. 28:50–79.

———. 1985b. ESS germination strategies in randomly varying environments. II. Reciprocal yield-law models. Theor. Pop. Biol. 28:30–116

Grime, J. P. 1979. *Plant strategies and vegetation processes*. Toronto: John Wiley.

Harper, J. L. 1977. *The biology of plants*. New York: Academic Press.

Hausenbuiller, R. L. 1978. *Soil science*, 2nd ed. Dubuque: Wm. C. Brown.

Howland, G. P. and M. E. Edwards. 1979. Photomorphogenesis of fern gametophytes. Pp. 394–434 in *The experimental biology of ferns*, ed. A. F. Dyer. New York: Academic Press.

Isikawa, S. and T. Oohusa. 1956. Effects of light upon the germination of spores of ferns II. Two light periods of *Dryopteris crassirhizoma* Nakai. Bot. Mag. (Tokyo) 69:132–137.

Klekowski, E. J., Jr. 1969. Reproductive biology of the Pteridophyta. III. A study of the Blechnaceae. J. Linn. Soc., Bot. 62:361–371.

Leck, M. A. and R. L. Simpson. 1987. Spore bank of a Delaware river freshwater tidal wetland. Bull. Torrey Bot. Club 114:1–7.

Lee, K. E. 1985. *Earthworms, their ecology and relationships with soils and land use*. New York: Academic Press.

Leon, J. A. 1985. Germination strategies. Pp. 129–142 in *Evolution: Essays in honour of John Maynard Smith*, ed. P. J. Greenwood, P. H. Harvey and M. Slatkin. New York: Cambridge.

Lloyd, R. M. and E. J. Klekowski Jr. 1970. Spore germination and viability in Pteridophyta: Evolutionary significance of chlorophyllous spores. Biotropica 2:129–137.

Mohr, H. 1956. Die Beeinflussung der Keimung von Farnsporen durch Licht und andere Faktoren. Planta 46:534–551.

Raynor, G. S., E. C. Ogden, and J. V. Hayes. 1976. Dispersion of fern spores into and within a forest. Rhodora 78:473–487.

Schneller, J. J. 1979. Biosystematic investigations on the lady fern (*Athyrium felix–femina*). Plant Systematics & Evolution 132:255–277.

Schraudolf, H. 1985. Action and phylogeny of antheridiogens. Pp. 75–80 in *Biology of pteridophytes*, ed. A. F. Dyer and C. N. Page. Edinburgh: The Royal Society of Edinburgh.

Steel, R. G. D. and J. H. Torrie. 1980. *Principles and procedures of statistics*. Toronto: McGraw–Hill.

Sugai, M. and M. Furuya. 1967. Photomorphogenesis in *Pteris vittata*. I. Phytochrome mediated spore germination and blue light interaction. Pl. Cell. Physiol. 8: 737–748.

TOMIZAWA, K., M. SUGAI, and K. MANABE. 1983. Relationship between germination and P_{fr} level in spores of the fern *Lygodium japonicum*. Pl. Cell Physiol. 24:1043–1048.

TOWILL, L. R. and H. IKUMA. 1973. Photocontrol of the germination of *Onoclea* spores. I. Action spectrum. *Pl. Physiol. 51:973–978.*

VIMMERSTEDT, J. P. 1983. Earthworm ecology in reclaimed opencast coal mining sites in Ohio. Pp. *229–240 in Earthworm ecology*, ed. J. E. Satchell. New York: Chapman and Hall.

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Cyathea stolzei × *ursina*, a Distinctive Tree Fern Hybrid from Costa Rica

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Recent field work and collections from the Atlantic lowlands of Costa Rica have revealed a hybrid between two exindusiate species of *Cyathea*. This hybrid is noteworthy because it combines the characters of two species that are rather dissimilar and morphologically distinctive. Both of the parents are acaulescent tree ferns of reduced laminar architecture; both are also rather rare and spottily distributed, known from relatively few collections, and one was described only four years ago (Stolze, 1984).

The hybrid in question is a cross between *Cyathea stolzei* A. R. Smith ex Lellinger [originally described as *Trichipteris pinnata* Stolze], from Costa Rica and Panama, and *C. ursina* (Maxon) Lellinger *[Trichipteris ursina* (Maxon) R. Tryon], occuring from Belize to Panama. Both parents and the hybrid were found growing together at the same locality: Costa Rica, Pcia. Heredia, Cerros Sardinal, ca. 2 km N of Chilamate de Sarapiquí (Finca La Martita), 10° 28′ N, 84° 04′ W, ca. 80–160 m, *Smith et al. 1780* (CR, MO, UC). *Cyathea stolzei [Smith et al. 1794* (CR, MICH, MO, NY, UC)] was a relatively common fern in the forest understory, while *C. ursina [Smith et al. 1814* (AAU, CR, MICH, MO, NY, UC)] was common in the forest and along trails, especially in somewhat swampy sites. A single plant of the hybrid was discovered growing along a trail at the edge of the forest. The area was one rather rich in ferns, with about 70 species collected, but the only other tree fern species that were found in the area were *Cyathea trichiata* (Maxon) Domin *[Trichipteris trichiata* (Maxon) R. Tryon], a species characterized by its bipinnate-pinnatifid fronds, abundantly hairy axes, and trunks several meters tall, and *C. multiflora* J. E. Smith, also with bipinnate-pinnatifid fronds, a small hemitelioid indusium, and trunks 1–2 m tall.

One additional collection of the hybrid has been seen from an adjacent property: Costa Rica, Pcia. Heredia, Finca El Bejuco, at southern end of Cerros Sardinal (N of Río Sarapiquí), Chilamate de Sarapiquí, ca. 100 m, 10° 27′ N, 84° 04′ W, *Grayum et al. 4613* (MO). With it also grew the putative parents, *C. stolzei (Grayum et al. 4608*, CR, MO, UC) and *C. ursina (Grayum et al. 4621* CR, MO). One additional tree fern was found at this site: *Cyathea microdonta* (Desv.) Domin; it is easily distinguished by its bipinnate-pinnatifid fronds and spiny rachis and costae. At El Bejuco, *C. stolzei* grows only on the ridgetops and upper slopes; *C. ursina* occurs only in the swampy stream bottom at the base of the ridge. The hybrid is in the intermediate zone—the lower slopes of the ridge. Of the two parental species, only *C. ursina* has been found from the fern-rich (173

TABLE 1. Comparison of *Cyathea stolzei*, *C. ursina*, and their Putative Hybrid. The plants scored, one per taxon, are those cited in Fig. 1, all from Finca La Martita.

Character	*C. stolzei*	Hybrid	*C. ursina*
Habitat	ridgetops and upper slopes	lower slopes of ridge	swampy creek-bottom at base of ridge
Stipe scale shape and size	ovate–lanceolate, 5 × 2 mm	lanceolate, 10 × 2 mm	linear–lanceolate, 10 × 1 mm
Stipe and rachis scale density	sparse to nearly absent	moderately scaly	densely scaly
Lamina reduction	lower pinnae longest or 1 pair slightly reduced	lower 3 or 4 pairs gradually reduced	lower 8 pairs gradually reduced
Lamina/stipe ratio	46/31	75/25	62/15
Lamina dissection	pinnae lobed ≤ 1/10 their width	pinnae lobed 1/3–1/2 their width	pinnae lobed ca. 3/4 their width
Lamina texture	thick, firm	intermediate	thin-herbaceous
No. pinna pairs	8	15–17	28
Distance between proximal pinnae	7 cm	4.5 cm	3 cm
Pinna shape	elliptic	intermediate	lanceolate
Ratio of longest to shortest pinna	11/8	12/5–16/5	8/3
Pinna articulation	pronounced	intermediate	slight
Costal scales	absent	few	numerous
Venation	lower 2 or 3 converging below sinus	lower converging near sinus	lower reaching margin above sinus

total species) area of La Selva, about 7 kilometers distant (Grayum & Churchill, 1987).

The putative hybrid is intermediate between the two parents in essentially all characters, especially including laminar cutting and blade outline, scaliness, number of pinna pairs, and venation (Table 1; Fig 1). It is also somewhat larger than either of the parents. Unfortunately, spores have been shed from specimens of the hybrid, so it has not been possible to determine whether or not they are well-formed or viable. Morphologically, the hybrid resembles most closely *Cyathea phalaenolepis* (C. Chr.) Domin, a rare species known only from Pacific coastal areas of Colombia and Ecuador. That species can be distinguished by its more deeply cut pinnae (incised ca. 3/4 their width), often numerous trichomes on the costa abaxially, and lack of reduced basal pinnae. It is tempting to speculate that *C. phalaenolepis* could have arisen through hybridization

FIG. 1. *Cyathea stolzei*, *C. ursina*, and their putative hybrid. A, frond outline of *C. stolzei* (*Smith et al. 1794*, UC). B, frond outline of *C. stolzei* × *ursina* (*Smith et al. 1780*, UC). C, frond outline of *C. ursina* (*Smith et al. 1814*, UC). D–F, pinna outlines of A–C, respectively. H–J, pinna segments of A–C, respectively. K–M, stipe base scales of A–C, respectively.

between *C. stolzei* and *C. ursina* and that the hybrid could have become stabilized and dispersed by the mechanism of autogamous allohomoploidy, described for other Cyatheaceae by Conant and Cooper–Driver (1980).

The three non-parental species of tree ferns found at the two sites are all very unlikely to have participated in the hybridization described herein because they are all more dissected (bipinnate-pinnatifid) and belong to different species groups within *Cyathea* (see Barrington, 1978; Tryon, 1976). Furthermore, they all have additional characters not shown in the hybrid, e.g., the indusiate condition in *C. multiflora*, the spininess of *C. microdonta*, and the pubescence, rhizome scales, and pale green color of *C. trichiata*.

Other hybrids have been reported in this group of *Cyathea (Trichipteris* of Barrington, 1978). Tryon (1976) listed one putative hybrid between *Cnemidaria* and *Trichipteris* from Grenada, six hybrids between *Cyathea* and *Trichipteris* from the Antilles and Central America, and three hybrids between *Cnemidaria* and *Cyathea* from the Antilles. Conant (1983) reported a number of hybrids in the genus *Alsophila* from the Greater Antilles. We subscribe to the recent reclassification of Cyatheaceae by Lellinger (1987) in which *Trichipteris* (often spelled *Trichopteris)* is reunited with *Cyathea*.

Cyathea stolzei, originally known only from the Panamanian type (Stolze, 1984), is now known from three additional Panamanian collections in addition to the Costa Rican ones cited above: Pcia. Panamá, Distrito Panamá, Cerro Jefe, *van der Werff & van Hardeveld 6989* (MO, UC); Pcia. Panamá, road past Cerro Azul, 20 km from jct. with road through Tocumen, *Mori & Kallunki 2191* (MO, UC); and Pcia. Colón, Santa Rita Ridge road, 8.3 mi E of Transisthmian Hwy., *McPherson 7464* (MO, UC).

The range of *C. ursina* is now known to extend into Panama: Pcia. Coclé, Caribbean side of divide at El Copé, 200–400 m, *Hamilton & Davidse 2677* (MO); Pcia. Coclé, between Caño Sucio and waterfall at base of Cerro Pife, Sytsma et al. 2545 (MO).

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Literature Cited

Barrington, D. S. 1978. A revision of the genus *Trichipteris*. Contr. Gray Herb. 208:1–93.

Conant, D. S. 1983. A revision of the genus *Alsophila* (Cyatheaceae) in the Americas. J. Arnold Arboretum 64:333–382.

——— and G. Cooper-Driver. 1980. Autogamous allohomoploidy in *Alsophila* and *Nephelea* (Cyatheaceae): A new hypothesis for speciation in homoploid homosporous ferns. Amer. J. Bot. 67:1269–1288.

Grayum, M. H. and H. W. Churchill. 1987 [1988]. An introduction to the pteridophyte flora of Finca La Selva, Costa Rica. Amer. Fern J. 77:73–89.

Lellinger, D. B. 1987 [1988]. The disposition of *Trichopteris* (Cyatheaceae). Amer. Fern J. 77:90–94.

Stolze, R. G. 1984. Two new tree ferns from Panama. Amer. Fern J. 74:101–104.

Tryon, R. M. 1976. A revision of the genus *Cyathea*. Contr. Gray Herb. 206:19–98.

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Dark-grown *Psilotum*

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Sporophytes of *Psilotum* are slow growing plants. This may be one reason why *Psilotum* has been subjected to very few experimental investigations. Marsden and Wetmore (1954) found that the apices of aerial stems grown in axenic culture often differentiated into rhizome apices. Rouffa (1966) observed that *Psilotum*, which was illuminated with cool white fluorescent light at 200–400 ft.-c. for extended periods of time, would produce unusual fertile appendages.

Warren H. Wagner, Jr. (pers. comm., 1986) observed unusual plants of *Psilotum* collected in Hawaii by Francis G. Howarth on the floor of a lava tube in complete absence of light. These plants had the appearance of short aerial rhizomes. The modifications of these plants were apparently caused by their growth in the dark, so Wagner suggested that such modified development might be produced experimentally by giving greenhouse-grown plants a dark treatment. The aim of this investigation was to determine whether *Psilotum* plants could grow at all for an extended period in the dark and whether their morphology would be altered by such growth.

MATERIALS AND METHODS

A plant of *Psilotum nudum* P. Beauv. growing in a clay pot with a diameter of 28 cm and a height of 26 cm has been cultivated in the greenhouse at Vanderbilt University for over 20 years. This large plant with an extensive rhizome system and over 150 aerial shoots was placed in a dark growth chamber in a dark room for one year. During the experiment the plant was watered 2 or 3 times a week and the temperature varied from 21–27° C.

After one year in the dark, a sample of the new aerial growth was removed and fixed in FAA. The plant was returned to the greenhouse to determine if it would continue to grow and if the new aerial growth would return to the typical *Psilotum* morphology. After 4 months in the greenhouse, the new growth was examined and fixed in FAA.

Thin hand sections were used to study the anatomy of the new aerial stems and to compare it with aerial stems formed in the light and rhizomes. Toluidine blue O was used as a general stain for the sections (O'Brien et al., 1964). Oil red O was employed to demonstrate lipid and lignin respectively in the sections. The terminology for *Psilotum* of Foster and Gifford (1974) has been employed for the descriptive aspects of this study.

Cell sizes are reported with the standard error of the mean. An analysis of variance and Duncan's multiple range test (Li, 1964) were used to determine if

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differences between the means were statistically significant. Means followed by different letters are significantly different to the 1% level.

Results

The initially green aerial stems remained green for the year in the dark. During this period these stems did not undergo any significant growth or unusual development. Since observations would have disturbed the soil around the plant, no effort was made to study rhizome growth. The main effort was to examine any new aerial growth formed in the dark.

The new aerial stems, which developed in the dark, differed from green aerial stems grown in the light (Figs. 1, 2). These aerial stems developed from rhizome apices that had turned toward the soil surface. The color of these cylindrical stems ranged from white to dark brown. The apices were white, and the stem color changed from yellow-brown below the apical region to dark brown in the older basal region (Figs. 1, 2).

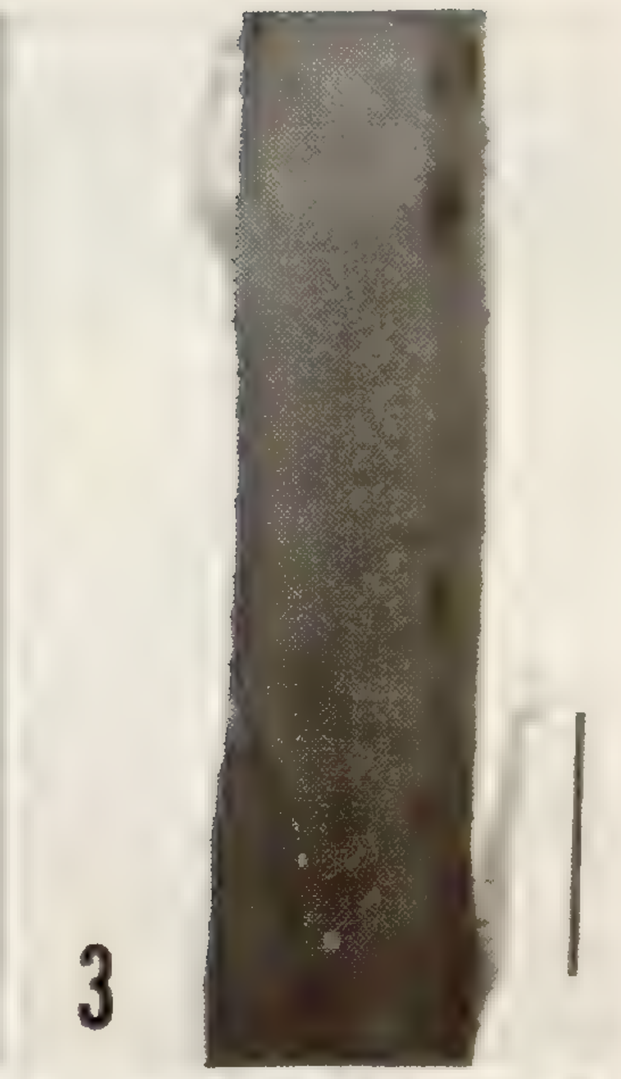
The basal portions of the main aerial stems differed from light-grown stems by bearing rhizoids (Fig. 3). The rhizoids were short, less than 200 μm long, and bicellular. Other portions of the dark-grown stems had stomata and occasional rhizoids. The stomata were similar in size and shape to those on green stems; however, there were about 1/10 the number per unit area on the dark-grown stems. Areas of the dark-grown stems with large numbers of rhizoids lacked stomata.

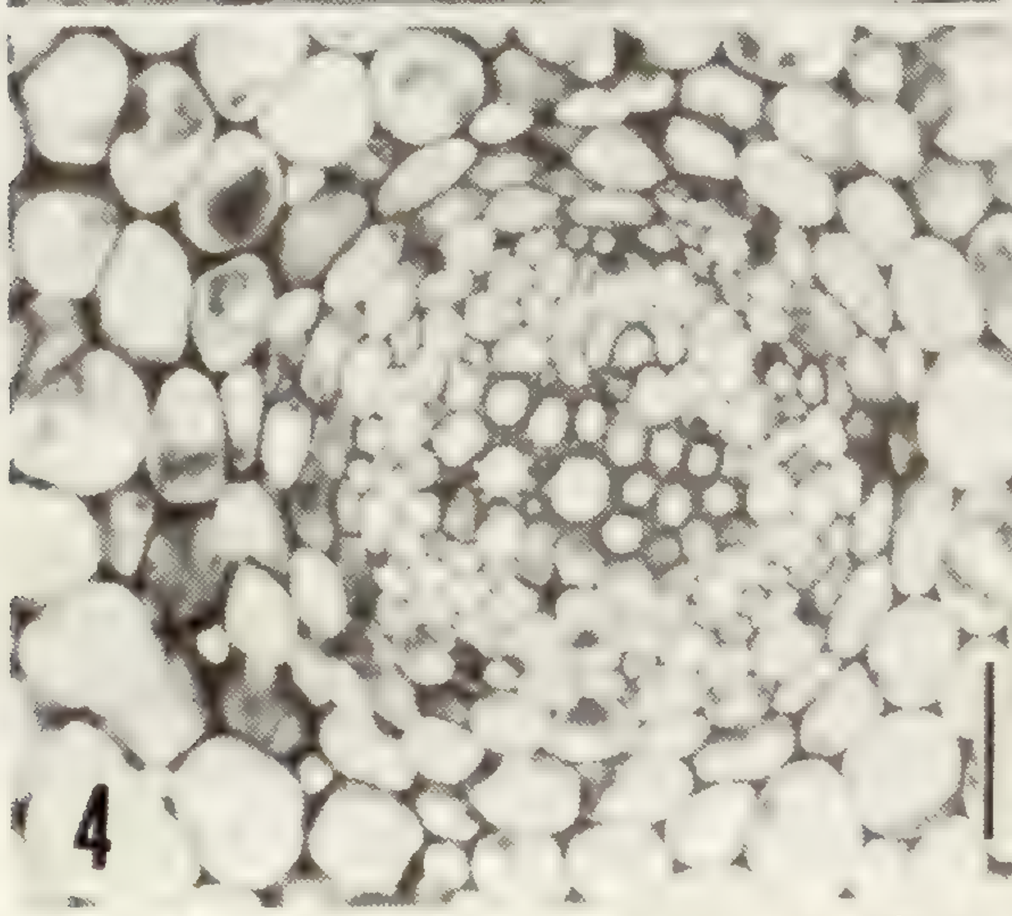
The apex of the main stem produced enations especially in the later stages of stem development (Figs. 1, 2, 3). The mature enations were about the same size as enations on green stems; however they were white instead of green.

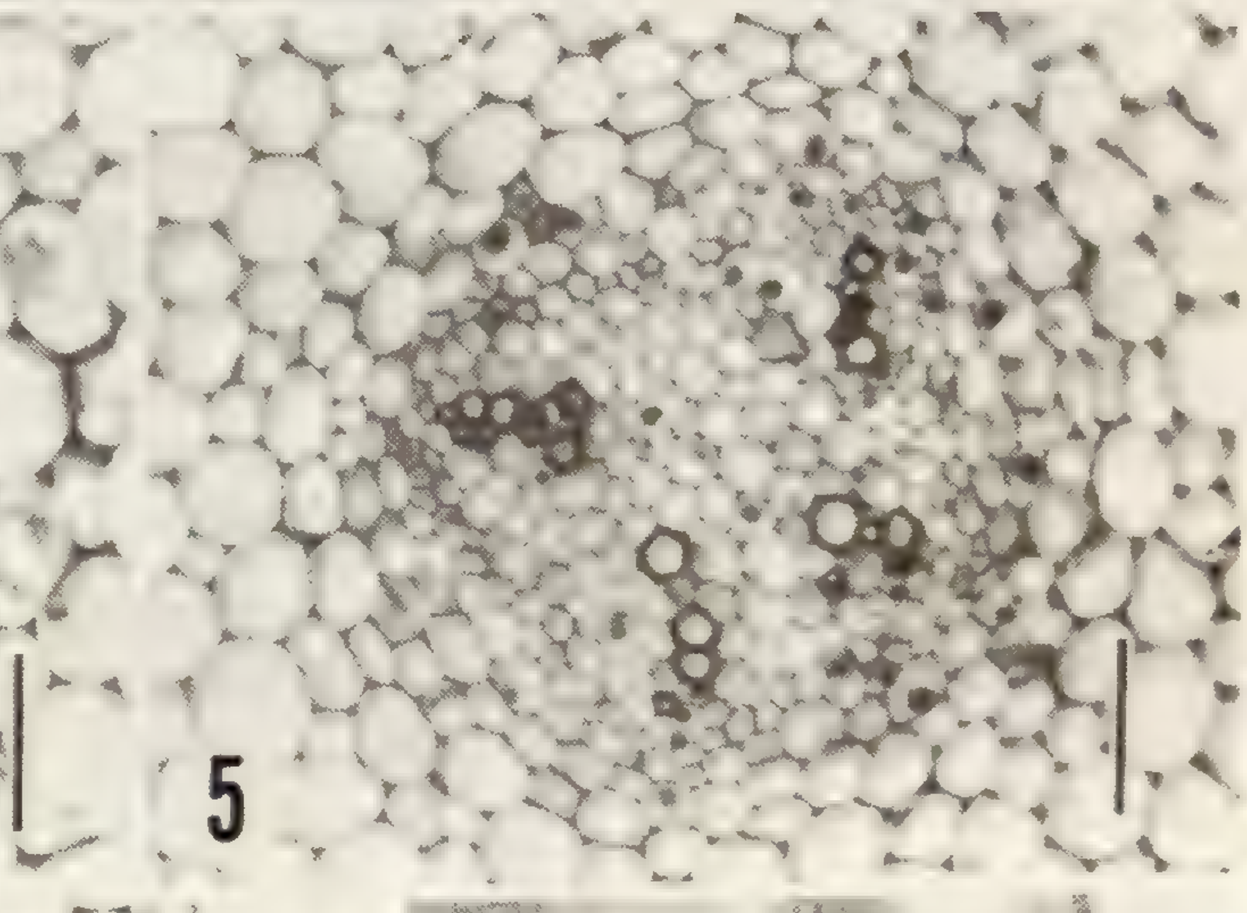
The main stems often branched but not dichotomously (Figs. 1, 2). A lateral branching resulted from meristematic areas along the stem. The lateral meristematic regions were connected by vascular tissue to the stele of the main stem. Stems with lateral branches had a modified cylindrical shape; stems became slightly fluted for a short distance above the lateral branches. Although the cylindrical shape was altered by the branches, the dark-grown stems never attained the fluted condition of green aerial stems grown in the light.

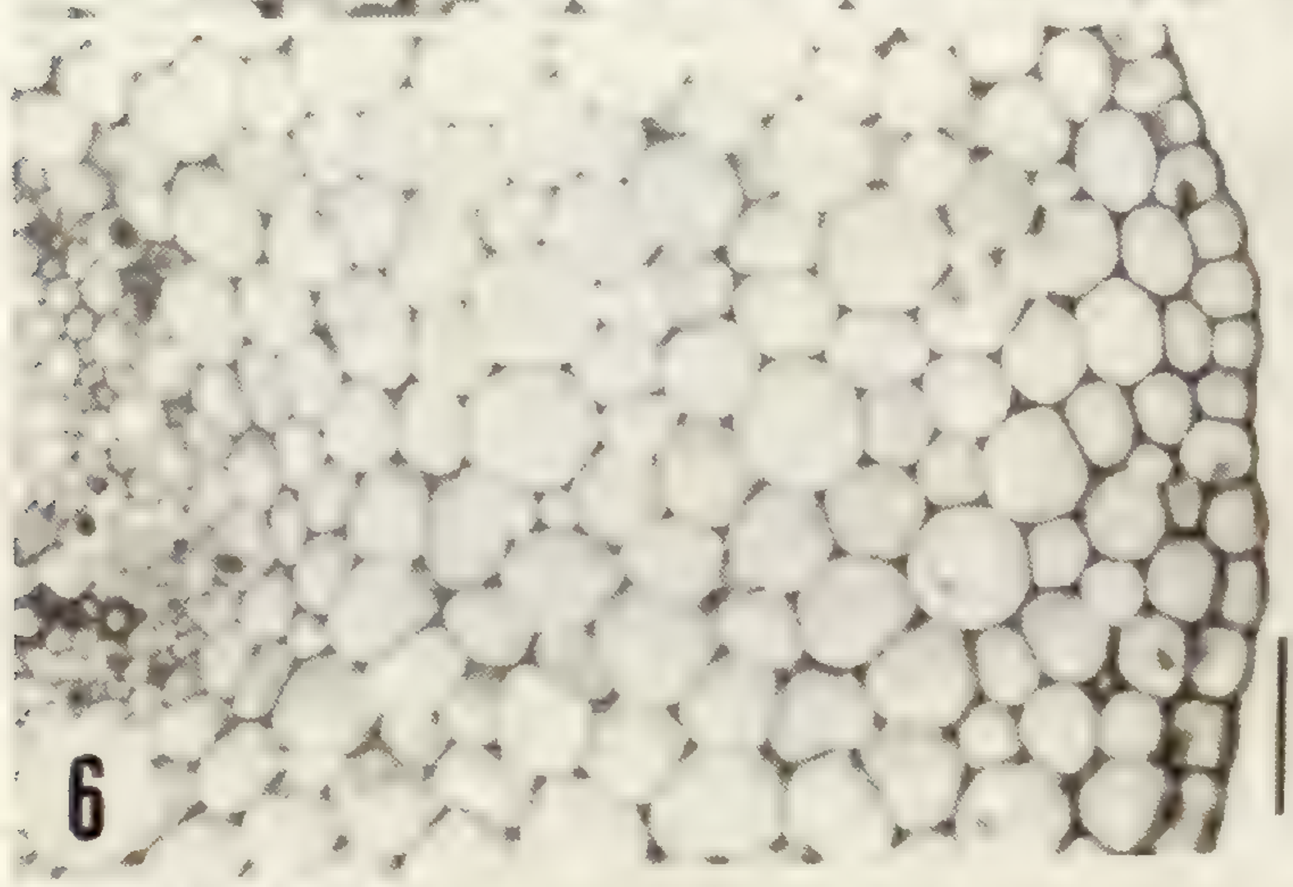
The development of the lateral branches repeated that of the main stems. The region of a lateral branch closest to the main stem had a cylindrical shape and often bore short rhizoids even though these areas were well above the soil. As the lateral branches became longer and increased in diameter, the rhizoids became infrequent. The shape of these branches remained cylindrical if no additional branching occurred.

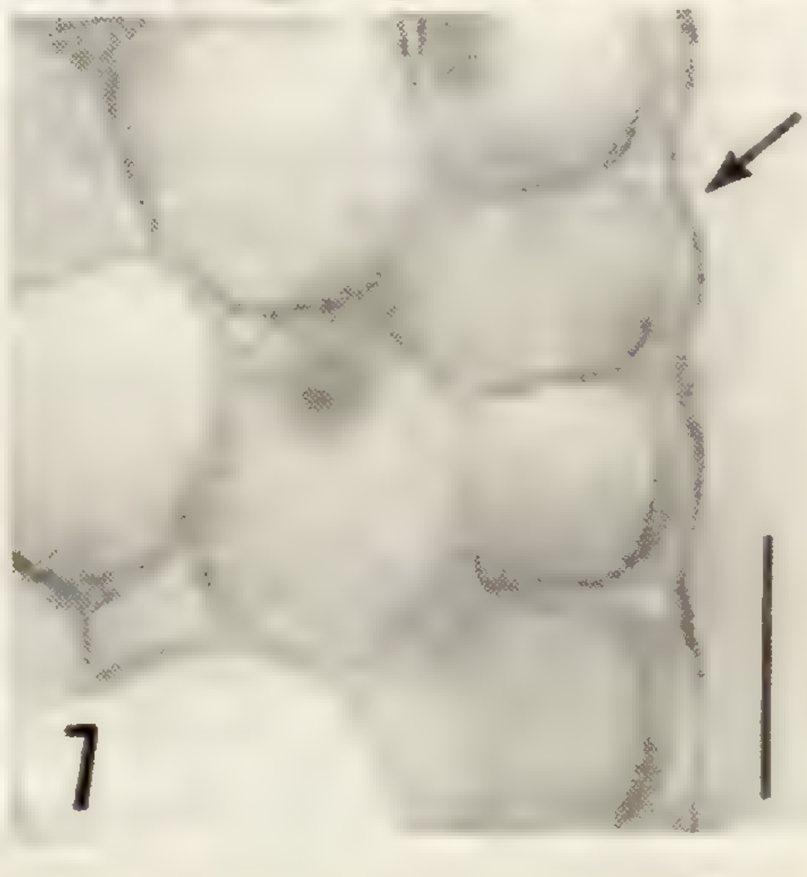
The internal structure of the dark-grown main and lateral stems was similar. The basal portions of the stems had protosteles (Fig. 4) and the cortex was composed of parenchyma cells. In the basal portions of the older stems, occasionally, some of the cortical cells had wall elaborations of phlobaphenes or condensed tannins (Fig. 8). The phlobaphene wall elaborations were similar to those often found in the cortical cells of *Psilotum* rhizomes and in the inner cortex of older light-grown stems. As long as the diameter of the stem and stele remained small, the stele was protostelic (Fig. 4). In most cases, the main and











FIGS. 1–7. The morphology and anatomy of dark-grown aerial stems of *Psilotum*. FIG. 1. Dark-grown aerial stems. Original green aerial stems have been removed to better demonstrate the dark-grown stems. Bar = 1 cm. FIG. 2. Apical regions of dark-grown stems. Arrows indicate young lateral branches. Bar = 1 cm. FIG. 3. Portion of dark-grown stem with short rhizoids and two enations. Bar = 2 mm. FIG. 4. Protostele of dark-grown stem. Bar = 100 μm. FIG. 5. Siphonostele with parenchymatous pith of dark-grown stem. Bar = 100 μm. FIG. 6. Parenchymatous cortex of dark-grown stem. Bar = 100 μm. FIG. 7. Epidermal cells of dark-grown stem with lipid (arrow) impregnated into thick outer walls. Oil red O staining. Bar = 50 μm.

lateral stems increased in diameter above their bases. Under these conditions the steles had a larger diameter and became exarch siphonosteles (Fig. 5), with isolated groups of xylem cells surrounding a parenchymatous pith. The cortex of the siphonostelic regions was composed of parenchyma cells (Fig. 6). Minor phlobaphene elaborations were rarely found in the walls of the inner cortex cells. There were no sclerenchyma or chlorenchyma cells in the stems grown in the dark.

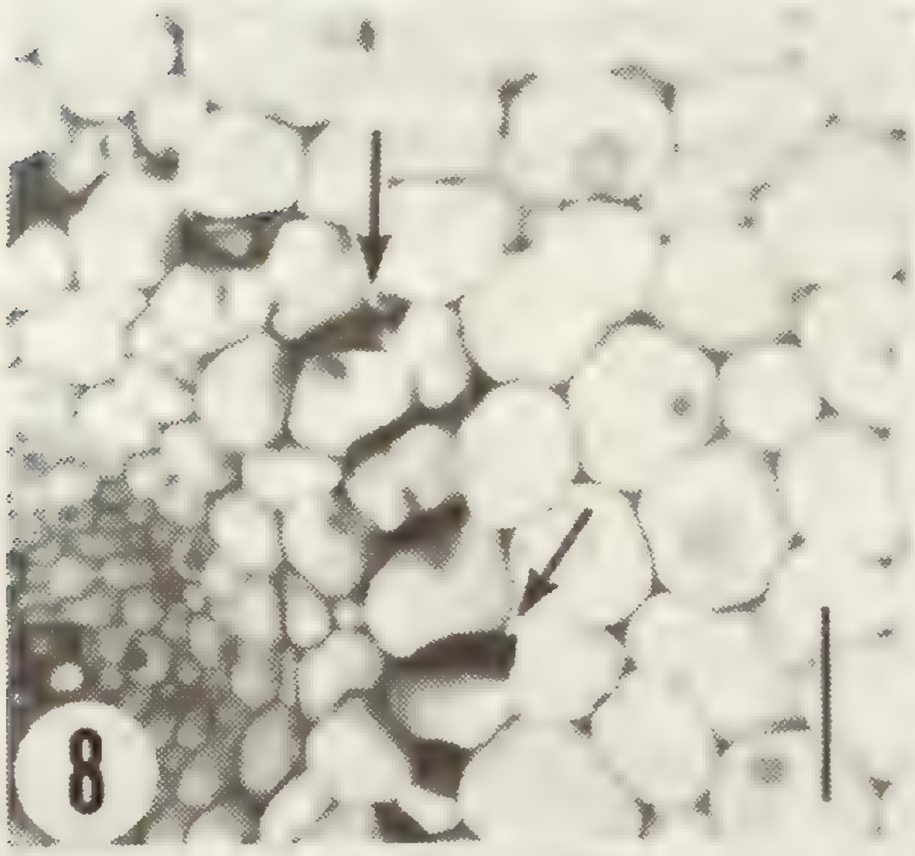
Because MacDougal (1903), Burkholder (1936), and Kolda (1937) found cell size differences between dark-grown and illuminated seed plants, the size of the cortical and epidermal cells of dark- and light-grown aerial stems and those of rhizomes were measured (Table 1). The length and width of the inner cortex cells of both types of aerial stems were essentially the same (Table 1). However, the cortical cells of the rhizome were shorter and wider than the cortical cells of the aerial stems. The epidermal cells of the aerial stems, dark- and light-grown, were not significantly different at the 1% level (Table 1). The surface cells of the rhizome did differ in size, again shorter and wider, from the epidermal cells of the aerial stems.

The epidermal cells of the dark-grown stems (Fig. 7) were more similar to those of the light-grown, green stems (Fig. 13) than those of the rhizomes (Fig. 9). The outer wall thickness of the epidermal cells of the dark-grown stems averaged about 8 μm. The outer 1 μm of this wall was impregnated with lipid materials (Fig. 7, arrow). Surface areas of the dark-grown stems with large numbers of rhizoids had epidermal cells with thinner (4 μm) outer walls. The epidermal cells of green stems (Fig. 13) had thicker outer walls (14 μm) with lipid material in the outer 2 μm of the wall in addition to cuticular material on the surface. The outer walls (about 2 μm thick) of the surface cells of the rhizome were only slightly thicker than the inner walls of these cells (Fig. 9). Also, these cells had only a very thin layer (0.5 μm) of lipid materials impregnated in the outer part of this surface wall.

The steles connecting the lateral branches to the main stems were protosteles. If the main stem had a protostele at the level of branching, the protostele branched to supply the lateral axis. If a siphonostele was present in the main stem, one or two bundles diverged to connect with the protostele of the lateral branch.

After one year in the dark, the plant was returned to the greenhouse. Some of the white apices of the dark-grown stems dried out under the less humid greenhouse conditions, but most of them continued to grow in the light. These apices, terminal and lateral, gave rise to dichotomously branched, green, fluted stems with enations (Figs. 10, 11). The large arrows in Figures 10 and 11 indicate where the terminal apices of main dark-grown stems produced the normal green stems under greenhosue conditions. Smaller arrows show where the apical meristems of lateral branches gave rise to the typical green aerial stems of *Psilotum*.

The internal anatomy of these green stems which developed from the dark-grown stems had the normal structure for aerial stems (Fig. 12, 13). These stems had stomata, a chlorenchymatous outer cortex, a sclerenchymatous middle cortex, and a parenchymatous inner cortex (Fig. 13). The steles for the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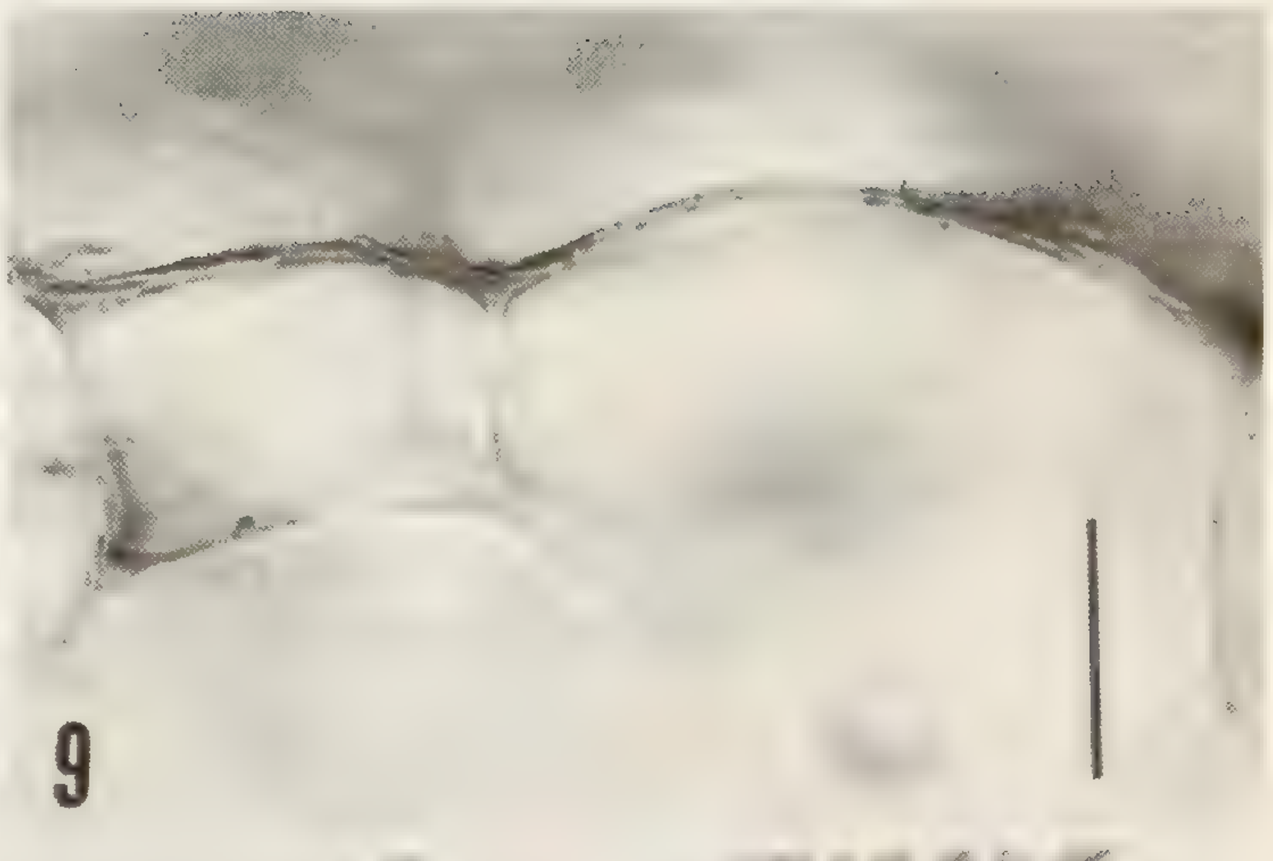
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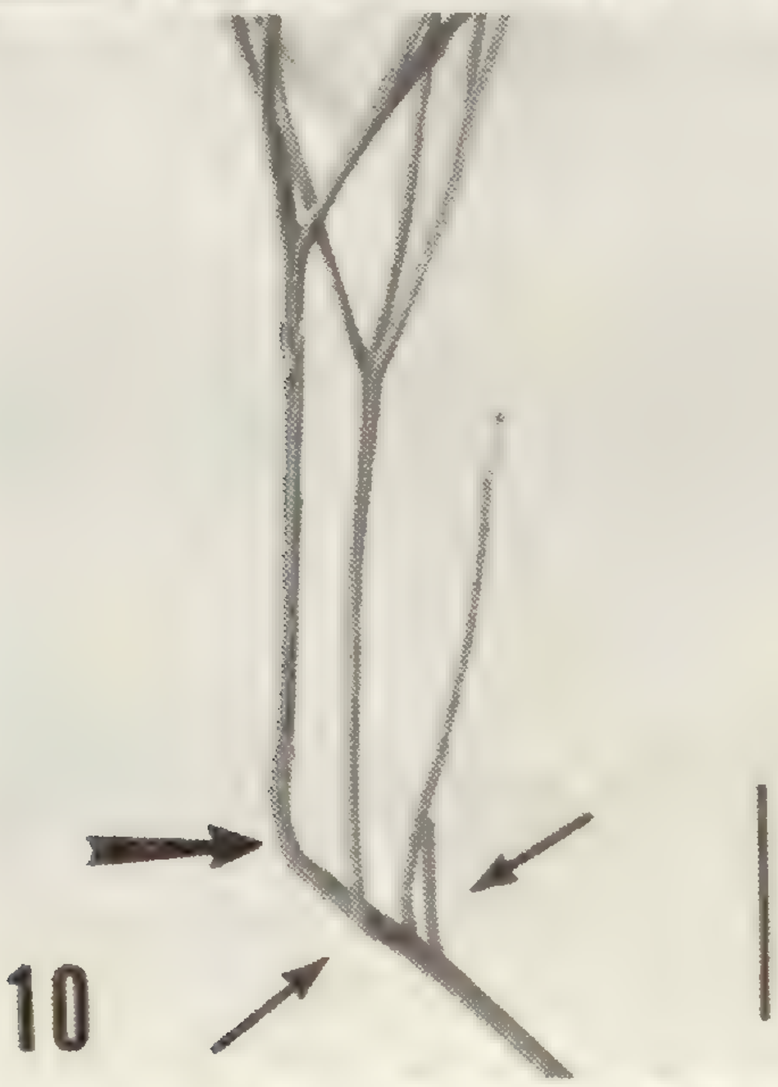
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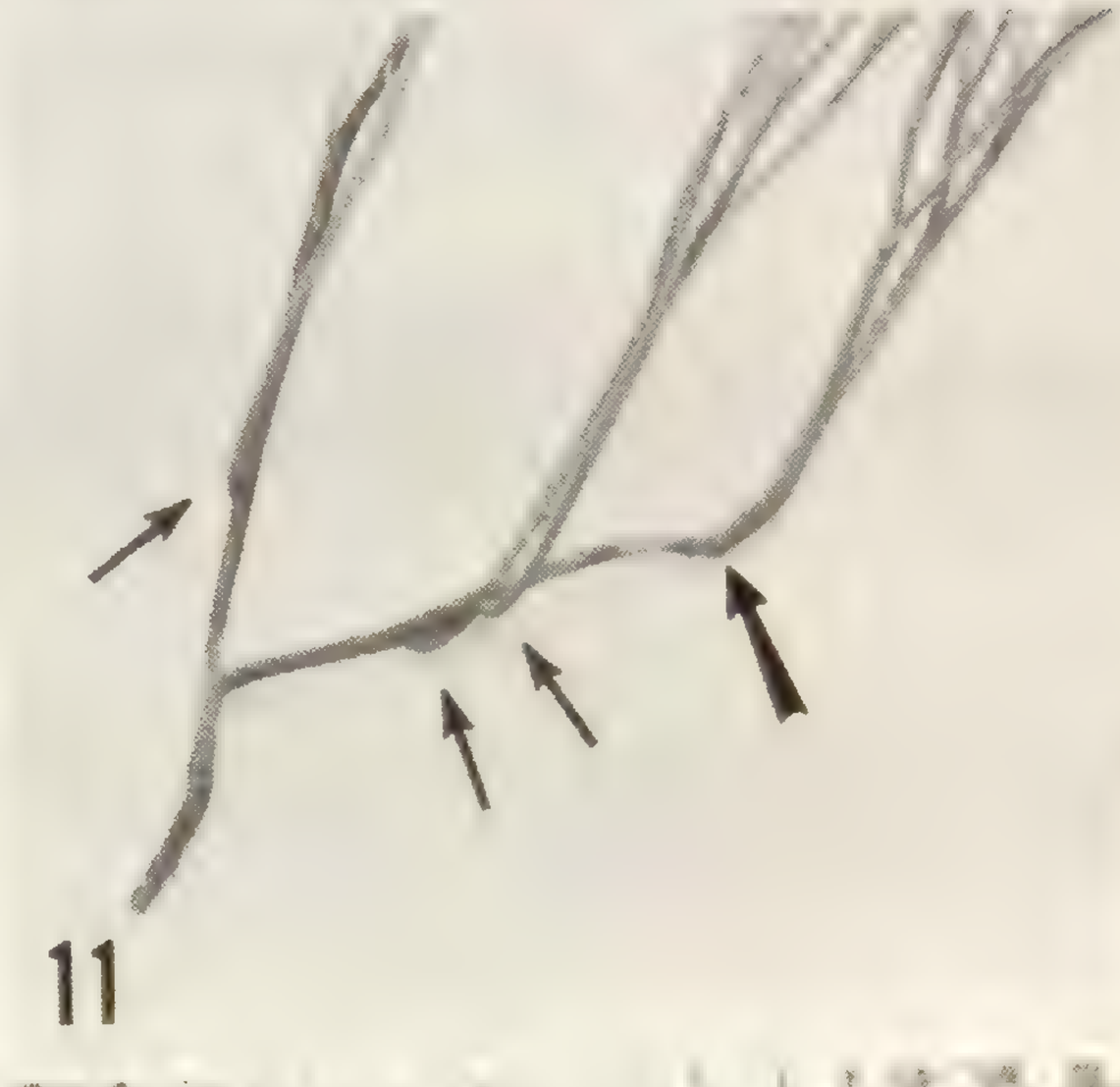
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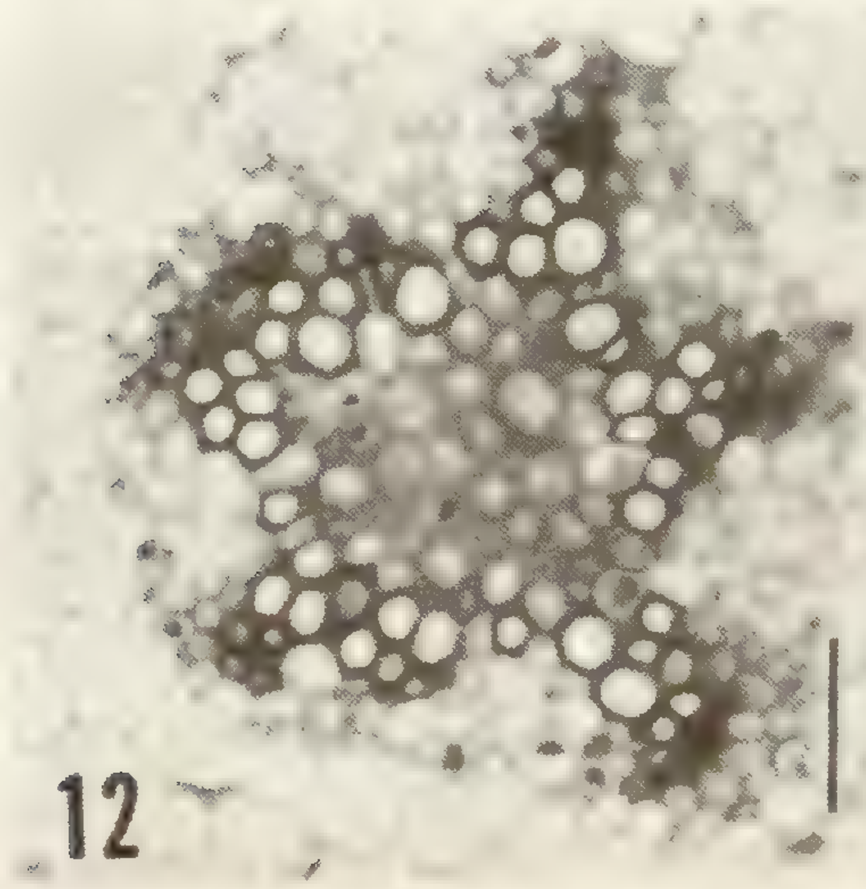
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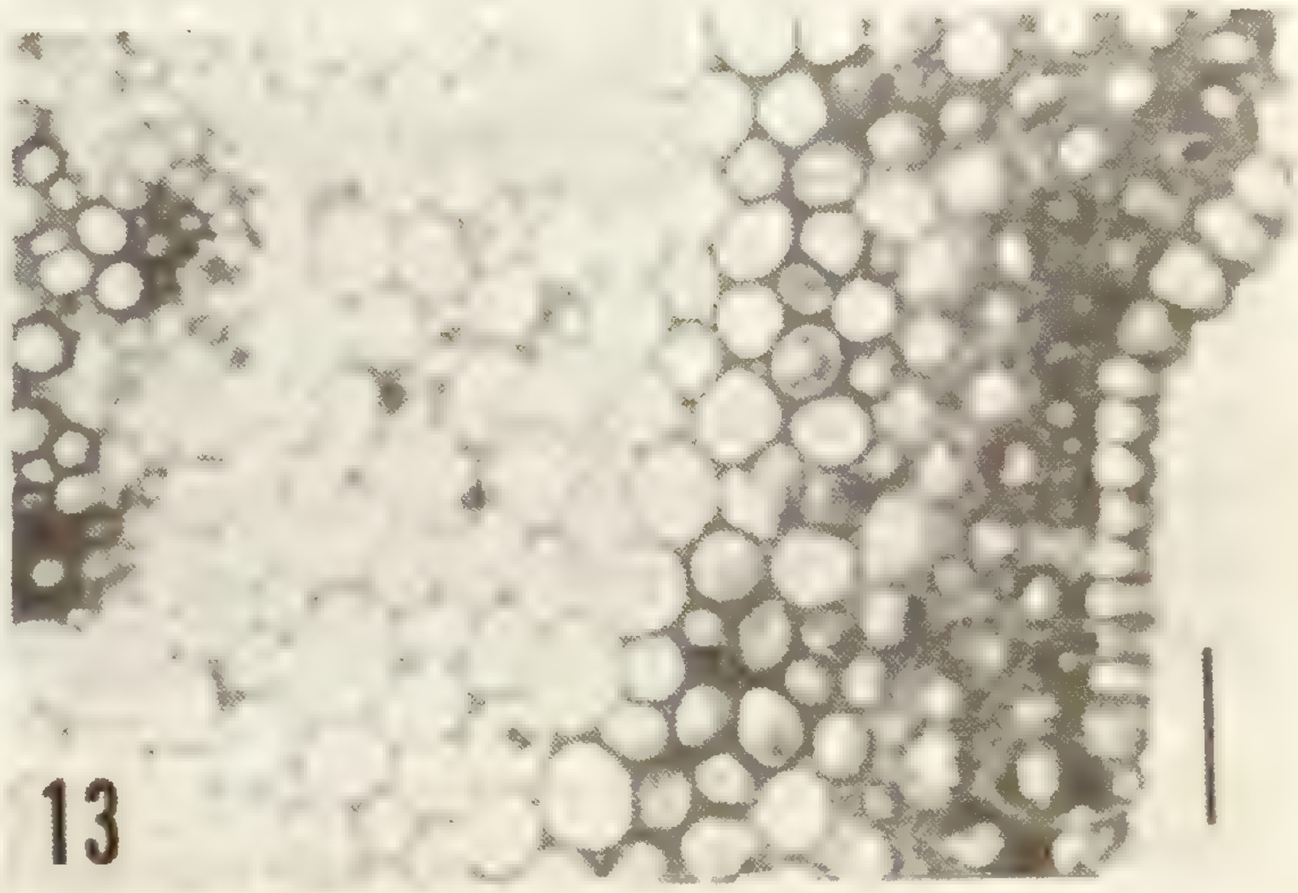
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FIGS. 8–13. Aspects of dark- and light-grown axes of *Psilotum*. FIG. 8. Phlobaphene wall deposits (arrows) in cortex cells of dark-grown stem. Bar = 100 μm. FIG. 9. Epidermal cells of *Psilotum* rhizome. Bar = 50 μm. FIGS. 10 and 11. Normal, green aerial stems growing from dark-grown aerial stems. Large arrows indicate where main apex of dark-grown stem became a green stem. Small arrows indicate where lateral branches of dark-grown stems became green stems. Bars = 1 cm. FIG. 12. Siphonostele with sclerenchymatous pith of a green stem which developed from a dark-grown stem. Bar = 100 μm. FIG. 13. Cortex and epidermis of a green stem which developed from a dark-grown stem. Bar = 100 μm.

TABLE 1. Cell Size Variation in *Psilotum* Axes. Measurements are in micrometers (μm).

Cell types	Green aerial	Brown aerial	Rhizome
Cortex			
Length	513.0 ± 9.5a	470.0 ± 16.1a	221.7 ± 6.8b
Width	53.1 ± 0.9a	56.9 ± 1.2a	111.3 ± 2.2b
Epidermis			
Length	256.3 ± 9.2a	245.6 ± 5.1a	131.9 ± 4.7b
Width	31.3 ± 0.7a	29.1 ± 0.5a	60.5 ± 2.0b

larger diameter green stem had the typical exarch siphonostele with groups of xylem cells surrounding a sclerenchymatous pith (Fig. 12). The smaller diameter tips of the green stems were normal with protosteles and no sclerenchyma tissue in the cortex.

DISCUSSION AND CONCLUSIONS

This *Psilotum* plant remained alive and continued to develop during the year of darkness. Many factors may have been involved in maintaining this green plant in the dark, however, three factors were assumed to be important. The demands for organic nutrients should be relatively small because *Psilotum* grows slowly, and the mycorrhizal fungus in the rhizome system should continue to supply nutrients even in the dark. Also, this large plant should have storage products available for growth.

Psilotum does not etiolate in the dark. The dark-grown aerial stems show no evidence of unusual elongation and, except for the absence of chlorophyll, the enations are unchanged. The cortical and epidermal cells in the dark-grown stems are essentially the same size as those from the light-grown, green stems. The overall brown color of these aerial stems further confirms that etiolation has not occurred.

The dark-grown stems have several charateristics exhibited by *Psilotum* rhizomes. They are brown, cylindrical, and bear rhizoids. In addition, these stems branch laterally which is a branching possibility for rhizomes but not for green aerial stems. However, if the general morphological appearance and not the absence of chlorophyll is considered, the dark-grown stems have more of a resemblance to normal aerial stems than to rhizomes.

The rhizoids on the dark-grown stems are very short and are not obvious to the naked eye even in areas with large numbers of rhizoids. Since most of the stem surfaces are almost devoid of rhizoids, the dark-grown stems lack the hairy appearance of rhizomes which are covered with long rhizoids. It is the smoothness of these aerial stems along with the presence of enations which make the dark-grown stems appear different from rhizomes.

Anatomically, the dark-grown stems have characteristics of the normal aerial stems. The shift from protostele to siphonostele is similar. Also, the xylem configuration in the exarch siphonostele is that of normal aerial stems. The

epidermal and inner cortex cell sizes are essentially the same for dark- and light-grown stems. Both types of stems have stomata and thickened outer epidermal cell walls even though there are fewer stomata and less of an epidermal wall thickening for the dark-grown stems.

The cortex and pith of the dark-grown stems vary from the green aerial stems. There is an absence of sclerenchyma cells in the middle cortex and the pith of the siphonostelic regions. This would appear to be due to the lack of light during development. Most seed plants have a reduction in mechanical tissue if grown in the dark (MacDougal, 1903; Burkholder, 1936; Kolda, 1937). Often seed plants also have reduced amounts of xylem tissue if grown in the dark (Kolda, 1937); however, this does not appear to have happened with *Psilotum*.

During normal development, rhizome apices give rise to the apices of aerial stems which form the above ground portions of *Psilotum*. The reverse (aerial stem apex to rhizome apex) is also known to occur. Marsden and Wetmore (1954) showed that the apices of aerial stems could become rhizome apices in sterile culture. Bierhorst (1971) described another method for converting the aerial stems into rhizome apices. He found that if young aerial stems were buried in soil, they would form rhizomes. The apical regions with their enations were modified to become rhizome apices. Also, under these conditions rhizoids could develop from the immature portions of buried aerial stems.

None of the green aerial stems became rhizomes during this experiment. The plant used in this experiment had completed its annual flush of growth at the time it was placed in the dark. Since the development of these green stems was essentially complete at the start of the experiment, it would have been difficult for rhizomes to form from them. If the experiment had been initiated before the development of the green stems was fully determined, there would have been a greater possibility for the apices of the young green stems to change their development.

Whether greenhouse-grown *Psilotum* can be experimentally caused to form other types of aerial growth is unknown at this time. Since the aerial rhizomes of *Psilotum* from the lava tubes are different from the aerial growths of this study, it appears that *Psilotum* can assume more than one form in the dark. Thus, it is possible that experimental conditions other than those used in this study could cause a different growth habit for greenhouse-grown *Psilotum* in the dark.

Acknowledgments

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Literature Cited

Bierhorst, D. W. 1971. *Morphology of vascular plants*. New York: Macmillan Co.

Burkholder, P. R. 1936. Role of light in the life of plants. II. The influence of light upon growth and differentiation. Bot. Rev. (Lancaster) 2:97–172.

Foster, A. S. and E. M. Gifford. 1974. *Comparative morphology of vascular plants*. 2nd Ed. San Francisco: W. H. Freeman and Co.

JENSEN, W. A. 1962. *Botanical histochemistry*. San Francisco: W. H. Freeman and Co.

KOLDA, A. 1937. Zur Anatomie etiolierter und periodisch belichteter Pflanzen und über die wirkung nachträglicher Kultur am Lichte. Beih. Bot. Centralbl. 57:319–380.

LI, J. C. R. 1964. *Statistical inference* I. Ann Arbor: Edwards Bros., Inc.

MACDOUGAL, D. T. 1903. The influence of light and darkness upon growth and development. Mem. New York Bot. Gard. 2:1–319.

MARSDEN, M. P. F. and R. H. WETMORE. 1954. In vitro culture of the shoot tips of *Psilotum nudum*. Amer. J. Bot. 41:640–645.

O'BRIEN, T. P., N. FEDER, and M. E. MCCULLY. 1964. Polychromatic staining of plant cell walls by toluidine blue O. Protoplasma 59:368–373.

PEARSE, A. G. E. 1968. *Histochemistry, theoretical and applied*. 3rd ed. Vol. 1. Baltimore: Williams and Williams Co.

ROUFFA, A. S. 1966. Induced *Psilotum* fertile-appendage aberrations. Morphogenetic and evolutionary implications. Canad. J. Bot. 45:855–861.

American Fern Journal 78(4): 117–121 (1988)

Experimental Studies on the Probability of Selfing by Protandrous Gametophytes

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Breeding systems have a significant influence on the genetic structure of populations (Allard et al., 1968; Baker, 1953; Jain, 1976; Wright, 1969). Many species of flowering plants exhibit mechanisms that prevent self-fertilization or increase the probability of cross-fertilization. These mechanisms usually function in the sporophyte generation and include heterostyly, dichogamy, and dioecy. In pteridophytes, the mating system is a function of the gametophyte generation. Unlike flowering plants, homosporous pteridophytes are faced with a potentially major evolutionary constraint due to the loss of genetic variation in progeny after a single generation of intragametophytic selfing. Klekowski (1972, 1973) hypothesized that homosporous taxa evolved a polyploid genetic system coupled with homoeologous chromosome pairing to compensate for the loss of variability due to selfing. The evidence that has accumulated to date suggests that this type of genetic system is not operative in most species (Buckley et al., 1985; Haufler, 1985). Analysis of genetic variation of sporophytes in natural populations by expression of recessive lethal genes and isozyme marker loci indicates that intragametophytic selfing and the resulting homozygosity are rare.

Mating systems in ferns are controlled both intragametophytically and intergametophytically. Intragametophytic factors include the temporal and spacial arrangement of gametangia and the presence of recessive lethal genes that prevent zygote development. Variations of gametangial development and occurrence include male to hermaphroditic, female to hermaphroditic, initially hermaphroditic, and sequentially unisexual. Intergametophytic factors are populational phenomena that relate to sex expression (e.g., dioecy, antheridiogens) and the density and availability of sperms. Of the intragametophytic factors, protandry (male to hermaphroditic gametangial sequence) has been hypothesized to have the greatest probability of intragametophytic selfing (Lloyd, 1974a).

The recent discovery of a recessive mutant allele for chloroplast packing in *Acrostichum danaeifolium* Langsd. & Fischer has provided an opportunity to test the probability of selfing in gametophytes with a male to hermaphroditic gametangial sequence.

MATERIALS AND METHODS

Spores were collected from a natural population in Florida, on U. S. Hwy. 41, 0.7 mile S of State Route 92 (*Lloyd 4790b*, BHO). Initial screening of gametophyte cultures indicated that spores from one sporophyte from this population yielded gametophytes of two distinct phenotypes. Spores from this sporophyte were sown and gametophytes grown on an inorganic nutrient

medium solidified with 1% agar (see Klekowski, 1969, for composition) in 100 × 15 mm petri dishes under continuous illumination by fluorescent and incandescent lamps. About ten days after germination and prior to sexual maturation, individual aseptic cultures were established in 60 × 20 mm petri dishes by placing gametophytes with different phenotypes immediately adjacent as follows: (1) pairs: one mutant (M) with one wildtype (WT); (2) one M with two WT; (3) one M with 3 WT; (4) one M with five WT; (5) one M with seven WT. In all cultures, wildtype gametophytes were placed equidistant from each other, between 0.5 and 1 cm from the side of the mutant gametophyte (e.g., in cultures 3–5, WT's form a triangular to circular pattern around the mutant). The number of replicate dishes for cultures 1–5 are, respectively: 45, 20, 15, 17, 16. Data from the composite culture reflect random sowing of spores without regard to placement (Table 2). The ratio of M:WT gametophytes in composite culture was not determined but for the purposes of this report it is assumed to be 1:1 (see Warne & Lloyd, 1987). Fertilization was facilitated by the addition of distilled water into each culture until much of the gametophyte tissue was covered with water, starting seven days following transfer and thereafter every 4 to 7 days for 55 days. Following fertilization the phenotype of the resulting sporophyte on the mutant gametophyte was observed to ascertain origin of the sperm effective in fertilization. Gametophyte ontogeny (Table 1) was studied by periodically sampling gametophytes grown in composite culture after random spore sowing. These gametophytes were mounted in Hoyer's medium mixed with aceto-carmine stain for observation.

Results

Genetics of the mutant phenotype.—Gametophytes expressing the mutant phenotype have a spotted appearance due to the packing of chloroplasts into one end of each cell. This expression is very similar to that of the "bar" mutation in gametophytes from irradiated spores in *Osmunda regalis* (fig. 4 in Howard & Haigh, 1968). Analysis of segregation patterns and expression of the mutant indicate that it is due to a single recessive allele (Warne & Lloyd, 1987). Sporophytes originating from selfed mutant gametophytes exhibited the same abnormal choroplast distribution; sporophytes produced from cross-fertilization with sperm from wildtype gametophytes exhibited normal chloroplast distribution.

Sequence of gametangial development.—In composite culture sexual development is fairly rapid. In both wildtype and mutant gametophytes, antheridia appear prior to archegonia in over 80% of those sampled (Table 1). Mutant gametophytes have a fairly prolonged antheridiate stage (8 to 19 days) prior to becoming hermaphroditic. Wildtype gametophytes have a slightly more rapid growth rate with a corresponding shortened unisexual antheridiate stage. Of the mutant gametophytes, 6.2% developed both gametangial types by the first date of sampling, and fewer than 5% were initially female. Wildtype gametophytes exhibited higher frequencies of initially female gametophytes.

TABLE 1. Sex Expression (%) in Gametophytic Cultures of *A. danaeifolium*, Mutant and Wildtype Phenotypes. DFS = Days from sowing; sowing density of 22 prothalli/cm²

	Mutant				*Wildtype*			
DFS	Neuter	Male	Female	Bisexual	Neuter	Male	Female	Bisexual
34	71.9	21.9	0	6.2	63.6	30.3	0	6.1
37	61.6	26.9	3.8	7.7	45.2	25.8	9.6	19.4
41	2.2	93.5	0	4.3	0	54.8	9.5	35.7
53	0	28.5	4.8	66.7	—	—	—	—

Spatial arrangement of gametangia was similar to that reported previously for this species (Lloyd & Gregg, 1975).

Mating system.—Experiments were designed to test the hypothesis that sporophyte ratios obtained following fertilization would result from random mating. Genotype frequencies can be predicted with the assumption of random mating within the experimental population and the goodness-of-fit to expectation may be tested by chi-square (X^2) analysis or calculation of exact probabilities (Sokal & Rohlf, 1969). The X^2 is a test of the null hypothesis that the observed genotype frequencies in resulting sporophytes do not differ significantly from those predicted by random mating. Three aspects of the mating system are of importance, proportion (density) of intra- and intergametophytic sperm, temporal/spatial arrangement of gametangia, and presence of recessive lethal genes (genetic load) which would prevent products of selfing from maturing into viable sporophytes.

To test for the presence of genetic load in this plant, 35 mutant and 35 wildtype gametophytes were isolated prior to sexual maturity and allowed to self. In all 70 gametophytes, viable sporophytes were produced. Therefore, it is concluded that such lethal genes are not expressed at stages that would confound the experimental results.

In testing proportion (density) of intra- vs. intergametophytic sperms on mating of gametophytes with a male to hermaphroditic gametangial sequence, analysis was made of observed vs. expected frequences of mutant vs. wildtype sporophytes on mutant gametophytes under the various culture regimes. Chi-square analysis (modified with Yates' correction for size classes fewer than five and sample sizes less than 200) and calculation of exact probabilities (for sample sizes fewer than 25) indicate that significant departures from expected frequencies due to random mating occurred in cultures 1, 2, 3, and the composite culture (Table 2). Cultures 1–3 are characterized by a ratio of from 1 to 3 WT to 1 M gametophyte and deviation from random mating is fairly uniform. In culture 4 (5WT:1M), the data suggest that a greater number of selfings occur than would be expected. In culture 5 (7WT:1M), sporophyte production approaches that consistent with random mating. From culture 1 and the composite culture to culture 5, as the proportion of WT to M gametophytes increases, there is a corresponding decrease in intragametophytic selfing (68–79% to 18% of mutant gametophytes).

TABLE 2. Analysis of Observed Sporophytic Frequencies on Mutant Prothalli Compared to Random-mating Expectations by Chi-square with Yates' Corrections (Culture 1 and Composite) or Calculation of Exact Probabilities (Cultures 2–5).

Culture	*Observed* Wildtype:Mutant	*Expected* Wildtype:Mutant	X^2 (df1)	P
1	14 : 31	22.5 : 22.5	5.68	0.01*
2	8 : 12	13.3 : 6.7	—	0.013*
3	6 : 9	11.25 : 3.75	—	0.004*
4	12 : 5	14.2 : 2.8	—	0.14
5	13 : 3	14 : 2	—	0.32
Composite	15 : 57	36 : 36	23.34	0.001*

* significant

DISCUSSION

If we assume that all gametophytes make equivalent number of sperms, in cultures 1–5, as intergametophytic sperm density increases the probability of intergametophytic mating increases. As these gametophytes express a male to hermaphroditic gametangial sequence, the results suggest that gametophytes with this gametangial sequence will have an increased probability of selfing unless they occur in populations with higher proportions of available intergametophytic sperms. In these populations, random mating will occur only when gametophyte density and spatial arrangements are such to offset the proximal advantage of sperms from a gametophyte to immediate access to newly maturing archegonia on that gametophyte. Therefore, the probability of random mating will increase in direct relationship to the increase in density of spore deposits. Due to the leptokurtic pattern of spore dispersal exhibited by ferns, the highest probability of random mating should be in the immediate vicinity of the parental spore source. Although random mating may occur under these conditions, inbreeding will most likely result as the vast majority of the spore population will originate from a single parent. Gametophytes that occur outside of the dense pattern have higher probabilities of selfing and isolated gametophytes must be obligately selfed.

If these results are applicable to natural populations, there should be an association between species whose gametophytes exhibit the male to hermaphroditic sequence and homozygosity at marker loci. There is a paucity of data from natural populations of ferns both in gametophyte gametangial sequences and genetic diversity and it is biased toward temperate taxa from larger populations. Most of the evidence to date indicates that populations are characterized by substantial amounts of genetic heterozygosity (Haufler, 1985). However, in almost all taxa studied, gametangial sequences, when reported, have been other than male to hermaphroditic. Two exceptions to this are lava flow plants of *Nephrolepis exaltata* in Hawaii, which exhibit a male to hermaphroditic sequence and are devoid of genetic load, suggesting an origin by selfing (Lloyd, 1974b), and species of *Ceratopteris*, which have very low levels of genetic load and a high frequency of individual homozygosity for

electrophoretic enzyme loci (Warne, 1985). However, gametophyte populations in *Ceratopteris* are diverse in gametangial sequences and may be mediated by an antheridiogen.

If homospory and the genetic homozygosity that result from selfing have been an evolutionary constraint in ferns, any adaptation that facilitates crossing will be selectively advantageous. It is not unexpected, therefore, that a large number of taxa exhibit gametangial sequences other than male to hermaphroditic, including those mediated by antheridiogens. As breeding systems are a major factor influencing the genetic structure of populations, and as autogamy in flowering plants has been suggested to be a derived feature and characteristic of taxa in specialized habitats (e.g., colonizers) or with short life-cycles, it can be hypothesized that selfing in ferns is also derived and limited to species in which genotype coherence has immediate reproductive advantage.

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Literature Cited

Allard, R. W., S. K. Jain, and P. L. Workman. 1968. The genetics of inbreeding populations. Advances Genet. 14:55–131.

Baker, H. G. 1953. Race formation and reproductive method in flowering plants. Symp. Soc. Exp. Biol. 7:114 – 143.

Buckley, D. P., R. M. Lloyd, K. M. Connolly, and T. Vierheller. 1985. Patterns of inheritance in *Onoclea sensibilis* L.: a test of the homeologous recombination system hypothesis. Amer. J. Bot. 72:920.

Haufler, C. H. 1985. Pteridophyte evolutionary biology: the electrophoretic approach. Proc. Roy. Soc. Edinburgh 86:315–323.

Howard, A. and M. V. Haigh. 1968. Chloroplast aberrations in irradiated fern spores. Mutat. Res. 6:263–280.

Jain, S. K. 1976. The evolution of inbreeding in plants. Annual Rev. Ecol. Syst. 7:469–495.

Klekowski, E. J. Jr. 1969. Reproductive biology of the Pteridophyta. III. A study of the Blechnaceae. J. Linn. Soc., Bot. 62:361–377.

_____. 1972. Genetical features of ferns as contrasted to seed plants. Ann. Missouri Bot. Gard. 59:138–151.

_____. 1973. Sexual and subsexual systems in homosporous pteridophytes: a new hypothesis. Amer. J. Bot. 60:535–544.

Lloyd, R. M. 1974a. Reproductive biology and evolution in the Pteridophyta. Ann. Missouri Bot. Gard. 61:318–331.

_____. 1974b. Mating systems and genetic load in pioneer and non-pioneer Hawaiian Pteridophyta. J. Linn. Soc., Bot. 69:23–35.

_____ and T. L. Gregg. 1975. Reproductive biology and gametophyte morphology of *Acrostichum danaeifolim* from Mexico. Amer. Fern J. 65:105–120.

Sokal, R. R. and F. J. Rohlf. 1969. *Biometry*. San Francisco: W. H. Freeman and Co.

Warne, T. R. 1985. Populational genetic variation in the homosporous fern genus *Ceratopteris* (Parkeriaceae). Ph.D. Diss. Ohio University, Athens.

_____ and R. M. Lloyd. 1987. Expression of a clumped-chloroplast mutant in the fern *Acrostichum danaeifolium*. Bot. Gaz. (Crawfordsville) 148:120–122.

Wright, S. 1969. *Evolution and the genetics of populations*, vol. 2: *The theory of gene frequencies*. Chicago: University of Chicago Press.

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A Preliminary Review of *Botrychium* in China

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The genus *Botrychium* has only recently received detailed attention. Since Clausen's monograph in 1938, most publications on this genus have been connected with floristic studies. Only Sahashi's study (1982) endeavored to take a broad, monographic approach. As is well known, the genus is difficult taxonomically because of subtle characters, variability, rarity, and few and often poor specimens of many of the taxa. Ideally the species should be studied in the wild as natural populations. Japan, western Europe, and North America are the areas best understood. China, on the other hand, has evidently been rather poorly collected, and a number of the taxa that were described by the great botanist R. C. Ching have been brought into question. For this reason, and in the hope of encouraging further investigations of Chinese *Botrychium*, we have prepared this preliminary review. We have maintained the genus intact, having recognized no segregate genera, and we have also used a conservative approach to species delimitation.

Through the kindness of Kunghsia Shing and the authorities of the Institute of Botany (PE), and the Institute of Forestry and Pedology (SFP), Academia Sinica, we were supplied with their *Botrychium* specimens for study. Dr. Shing kindly translated the labels. We also used specimens from the New York Botanical Garden (NY). University of Michigan (MICH), United States National Herbarium (US), Harvard University (A/GH), and University of California Berkeley (UC). Where Clausen had only 13 Chinese specimens to study, we had 191. DeVol (1945) listed only three species from east central China. A number of the taxa that had been proposed by R. C. Ching were synonymized in keeping with our present knowledge of variability in the genus. We extrapolated our knowledge of the variations of related New World species to arrive at our conclusions. Most of the taxa that have been reduced to synonymy were segregates of two species, *B. lanuginosum* and *B. robustum*.

The twelve species that we recognize in China display a diverse array of geographical ranges (Fig. 1) correlated with topography, climate, and agricultural activities. We did not map the records from the literature because of the chances of misidentification. The natural distribution of the species is limited to the southeastern half of the moist territory roughly separated by the line (Fig. 2) from the Da Hinggan Mountains to the Taihang Mountains to the Qingling Mountains, to the eastern and southern edges of the Qing-Zang Plateau (Inst. Bot., 1974; Chen et al., 1986; Ching, 1959; and Wu, 1983). An exception is *B. lunaria*, in Xinjiang Province, northwest China (not shown in Fig. 1), where the precipitation is higher on the north-facing slopes of the mountains (Wu et al., 1980). Within the major distribution area of *Botrychium*, annual precipitation is

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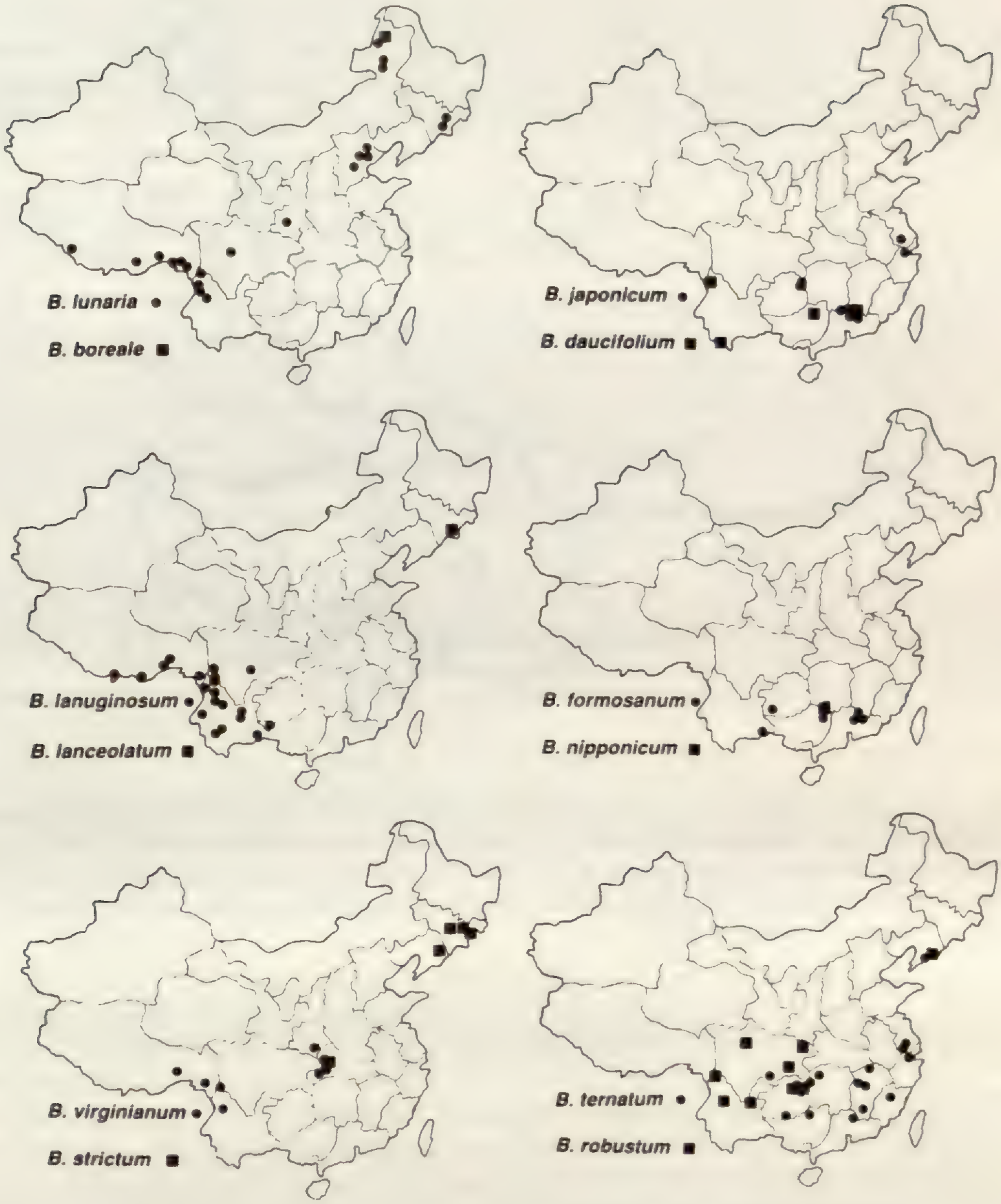

FIG. 1. Distribution of *Botrychium* species in China. Based on specimens seen by the authors.

usually greater than 400 mm. Elevation ranges from several hundred meters to 1000 m in the hilly regions of southeastern China. It increases to 1000–2000 m in the Loess Plateau and Yunnan-Guizhou Plateau, and finally reaches 4000 m at the eastern and southern edges of the Qing-Zang Plateau (Wu et al., 1983).

The ranges of the species in China are also characterized by disjunctions within a given geographical region. This is due apparently to intensive agricultural activities. Almost all flat lands in plains, basins, and even in mountainous regions have been cultivated for centuries for various crops. Only the mountains were left for non-agricultural usage, but even the slopes of these

FIG. 2. Diagram of Chinese *Botrychium* distribution. Heavy line = western border of all species (*B. lunaria*). A, cold temperate (*B. boreale*). B, Warm temperate (*B. lanceolatum*, *B. strictum*). C, East-central subtropical (*B. japonicum*, *B. ternatum*). D, Western subtropical (*B. lanuginosum* to the southwest, *B. robustum*, *B. virginianum* to the northeast). E, Southern subtropical (*B. formosanum*, *B. daucifolium*, *B. nipponicum*).

were used for tea plantations and for other crops. Most specimens from China were collected in the mountains. If there is a disjunction between two mountain regions, then there is a disjunction in range. For instance, the highly agricultural Sichuan Basin separates the distribution of *B. virginianum* into two regions, one in Hubei province, the other in Yunnan and Guizhou provinces (Fig. 1).

Seven geographical distribution groups can be recognized on the basis of the materials we have studied, two in the temperate zone, four in subtropics, and one very widespread. *Botrychium boreale* appears in the Da Hinggan Mountains in far northeastern China. *Botrychium lanceolatum* and *B. strictum* together comprise a group ranging in central and southern temperate zones. *Botrychium ternatum* and *B. japonicum* occupy the east-central subtropical areas, whereas *B. robustum* and *B. virginianum* are scattered in the western subtropical area. *Botrychium lanuginosum* grows at high elevations in Yunnan-Guizhou Plateau and in the southeast corner of the Qing-Zang Plateau. To the far south, *B. formosanum*, *B. daucifolium*, and *B. nipponicum* occur in the Nanling Mountain region—the southern subtropical area. The most interesting distribution is that of *B. lunaria*, which extends all the way from the Da Hinggan

Mountains in northeastern China to the south edge of the Qing-Zang Plateau. The range of *B. lunaria* provides the western boundary for the occurrence for all the Chinese botrychiums (Figs. 1, 2). Northward and westward from this line, grasslands, and sand and gravel deserts prevail, except to the far northwest, where we have two records of *B. lunaria* (see below, species 1). Of the 12 species credited to China below, *B. boreale*, *B. lanceolatum*, *B. formosanum*, and *B. nipponicum* are the first reports for this country.

In the enumeration to follow, we have listed only the synonyms that have been used for the respective species in China, with some additions where these seem necessary for clarification. For illustrations we have used various sources, Chinese or otherwise. The collection data have been abbreviated; numbers in parentheses following province names indicate numbers of collections seen from that province. The discussions under each taxon are aimed at calling attention to taxonomic problems, ecology, and human uses. We used C. Y. Wu's "Vegetation of China" to estimate parameters such as rainfall and temperature in the different zones.

Key to *Botrychium* of China

1. Leaf small, 3–15 cm long; leaf primordium glabrous; trophophore (sterile blade) pinnate or ternate, 1–2-pinnate.
   2. Pinnae fan-shaped, the pinna midrib absent. . . . . 1. *B. lunaria*
   2. Pinnae elongate, the pinna midrib present.
      3. Pinnae rounded at apex, often overlapping; primordial blade erect. . . . . 2. *B. boreale*
      3. Pinnae pointed at apex, usually well separated; primordial blade bending over. . . . . 3. *B. lanceolatum*
1. Leaf medium to large, mostly greater than 10 cm long; leaf primordium usually hairy; trophophore ternately 2–4-pinnate.
   4. Sporophore stalk joined to the trophophore stalk at or above the base of the trophophore blade.
      5. Sporophore stalk joined to the rachis above the base of the trophophore blade, somewhat variable in positon; leaf very hairy to essentially glabrous. . . . . 4. *B. lanuginosum*
      5. Sporophore stalk joined to the base of the trophorphore blade; leaf nearly to entirely glabrous.
         6. Ultimate segments contracted at the base, deeply divided; sporangia on 2–3-pinnate sporophore; sporangial cluster deltate. . . . . 5. *B. virginianum*
         6. Ultimate segments not contracted, shallowly lobed; sporangia on 1-pinnate sporophore; sporangial cluster narrowly linear. . . . . 6. *B. strictum*
   4. Sporophore stalk joined to the trophophore stalk below the base of the trophophore blade.
      7. Leaves sparingly hairy; leaf primordium with many fine hairs; blade mostly large, 10–25 cm long.

8. Sporophore stalk joined to the trophophore stalk near the base of the frond. . . . . 7. *B. japonicum*
8. Sporophore stalk joined to the trophophore stalk ca. 1/3–2/3 from base to trophophore blade.
   9. Trophophore blade up to 3-pinnate, chartaceous; sporophore stalk arising ca. 1/2–2/3 of the way from base to the trophophore blade. . . . . 8. *B. daucifolium*
   9. Trophophore blade up to 4-pinnate, herbaceous; sporophore stalk arising ca. 1/3–2/3 of the way from base to the trophophore blade. . . . . 9. *B. formosanum*
7. Leaves mostly glabrous; leaf primordium glabrous or only the upper part hairy; blade mostly smaller, 5–15 cm long.
   10. Terminal pinnules large, differentiated from lateral pinnules, 8–15 mm long, 5–10 mm wide, elongate, acute; margins finely serrate; fronds mostly turning red-brown in winter. . . . . 10. *B. nipponicum*
   10. Terminal pinnules smaller, more or less conform with the lateral pinnules, 3–10 mm long, 2–8 mm wide; rounded to truncate at the apex; margins nearly entire to finely dentate; fronds mostly green in winter.
      11. Segments blunt, rounded or subacute; margins entire to shallowly and coarsely crenate or dentate; trophophore leathery. . . . . 11. *B. robustum*
      11. Segments mostly acute; margins shallowly to deeply denticulate; trophophore herbaceous. . . . . 12. *B. ternatum*

1. *Botrychium lunaria* (L.) Sw., J. Bot. (Schrader) 2(1):110. 1802.

Illustrations: Inst. Bot. (1974, p. 31); Ching (1959, p. 17); DeVol et al. (1975, p. 66).

Representative Specimens: **Nei Monggol (Inner Mongolia)** (2 coll. seen). Da Hinggan Mts., *Z. Wang et al. 1506* (PE). **Jilin** (2). Changbai Mt., *T. N. Liou et al. 1633* (PE). **Hebei** (6). Chengde, *Nan Kai 430* (PE). **Shanxi** (3). Taibai Mt., *T. N. Liou et al. 2209* (PE). **Xinjiang** (2). Yili Zhaosu, *A. R. Li et al. 10496* (PE). **Sichuan** (1). Maerkang, *Z. Y. Wu 32726* (PE). **Yunnan** (5). Zhongdian, *K. M. Feng 1689* (A/GH). **Xizang (Tibet)** (8). Chayu, Demola Mt., *Oing Zang Team 731215* (PE).

This species is not only the most widespread but apparently the most common *Botrychium* (Fig. 1). This is no surprise, as this plant, the familiar moonwort of English-speaking countries, is the most cosmopolitan of all members of the genus, completely circumboreal and reappearing in southern South America, New Zealand, and Australia. *Botrychium lunaria* is known in Xinjiang Province but without specific locality (PE). It should be noted that this area in northwestern China, widely separated to the west from the other localities, is in a different drainage system. The moonwort is a very distinctive plant with its broadly fan-shaped, simple segments, and it is quite uniform, varying mainly in size and in occasionally producing dentate or incised pinnae.

This species extends from northeastern to southwestern China over many degrees of latitude. It requires substantial precipitation, 400–500 mm per year, and grows in mountainous regions at elevations of 1300–4000 m. Its various

FIG. 3. Silhouettes of selected Chinese *Botrychium* species. a, *B. lanuginosum*. b, *B. nipponicum*. c, *B. robustum*. d, *B. boreale*. e, *B. lanceolatum*.

habitats include semi-moist forest areas or fields: *Betula* forest, *Abies* forest, grasslands, and open stony pastures.

2. *Botrychium boreale* Milde, Bot. Zeit. (Berlin) 15:470, 880. 1857.

Illustrations: Fig. 3d; Sahashi (1978, p. 52).

Collections Examined: **Nei Monggol (Inner Mongolia).** Da Hinggan Mts., *Wang et al. 1506* (same data for other sheet of *B. lunaria*, PE).

Closely related to the much more common *B. lunaria*, this far northern species differs in its ascending, rather pointed pinnae. The occurrence of *B. boreale* in China has evidently not been reported previously. After earlier identifications as "*B. lunaria*," "*B. lunaria* var. *subincisum*," and "*B. ramosum*" (syn. of *B. matricariifolium*), this collection was finally identified correctly by J. Z. Wang in 1981. The three specimens of the single collection are entirely typical of the species as it occurs across northern Europe, especially in Scandinavia. The North American plant confused in the past with it [as *B. boreale* subsp. *obtusilobum* (Rupr.) Clausen] is a distinct species, *B. pinnatum* St. John (Wagner, unpubl.). Thus far, typical *B. boreale* has not been found in North America.

This species grows in grasslands scattered with birch trees in the Da Hinggan Mountains (Fig. 1) at an elevation of about 1000 m. Average January temperatures range from –28 to –38°C and average July temperatures from 16 to 20°C. Average precipitation is 400–500 mm. No doubt, further exploration in this cold region will reveal other populations, these often mixed with *B. lunaria*.

3. *Botrychium lanceolatum* (J. Gmelin) Angström, Bot. Not. 68, 1854.
Botrychium manshuricum Ching, Fl. Reipubl. Pop. Sin. 2:329. 1959.–ISOTYPE: Jilin, Changbei Shan, Fusong Xian, *N. T. Liou 1663* (PE!).
Botrychium ramosum Wang Wei et al. in N.T. Liou, Fl. Pl. Herb. Chinae Bor.–Orient. 1:21, fig. 23. 1958 (non *B. ramosum* Asch., 1864).

Illustrations: Fig. 3e; Tagawa (1959, p. 42).

Collections Examined: **Jilin.** Tizhi River, Changbai Mt., *T.N. Liou et al, 1663* (another sheet with same data at SFP is *B. lunaria*); *W. Wang et al. 2386* (SFP).

This species is reported here for the first time from China. Evidently very rare and local, it is known from only two localities, both on Changbai Mountain (Fig. 1). Both collections were first identified as *B. ramosum* Asch. (synonym of *B. matricariifolium* A. Braun), a fairly common amphiatlantic species of western Europe and eastern North America. *Botrychium lanceolatum* has a much broader range, being practically circumboreal at high latitudes. It differs from *B. matricariifolium* in its triangular rather than oblong trophophore, its shiny dark green rather than dull whitish green color (when alive), and its short, basally branched rather than tall, more distally branched sporophore.

4. *Botrychium lanuginosum* Wallich ex Hook. & Grev, Icon. fil. 1, pl. 79. 1831. –*Botrypus lanuginosum* (Wallich ex Hook. & Grev.) Ching in Shing, Glossary terms and names ferns 37. 1982.
Botrychium yunnanense Ching, Fl. Reipubl. Pop. Sin. 2:329. 1959. –*Botrypus yunnanense* (Wallich ex Hook. & Grev.) Ching in Shing, Glossary terms and names ferns 37. 1982. –TYPE: Yunnan, Dali, *Ducloux* 55 (PE!).
Botrychium decurrens Ching, Fl. Reipubl. Pop. Sin. 2:329. 1959. –*Botrypus decurrens* (Ching) Ching in Shing, Glossary terms and names ferns 37. 1982. –TYPE: Sichuan, without locality, *West China Academy Science 4729* (PE!).
Botrychium modestum Ching, Fl. Reipubl. Pop. Sin. 2:329. 1959. –*Botrypus modestus* (Ching) Ching in Shing, glossary terms and names ferns 37. 1982. –TYPE: Yunnan, Deqing, Chizhung, *K. M. Feng 5668* (PE!).
Botrychium parvum Ching, Fl. Reipubl. Pop. Sin. 2:330. 1959. –*Botrypus parvus* (Ching) Holub, Preslia 45:277. 1973. –TYPE: Guizhow, without locality, *S. W. Tang 41679* (PE!).

Illustrations: Fig. 3a; Ching (1959, pl. 2).

Representative Specimens: **Guangxi** (3). Linyin, Miao Mts., *R. C. Ching 24772* (PE). **Yunnan** (24). Kong Mt., *C. W. Wang 67157* (PE). **Sichuan** (2). Shimian, *J. S. Yin 4672* (PE), **Hunan** (1). without locality, *G. Z. He 4856* (PE). **Xizang (Tibet)** (8). Zhayu, *T. P. Yi 79162* (PE). **Guizhow** (1). without locality, *S. W. Tang 41679* (PE).

Clausen (1938) pointed out that "*B. lanuginosum* is decidedly variable in texture and the amount of pubescence of the leaf." We might add that this species is also extremely variable in size, the fertile leaves ranging from 10 to 75 cm tall. The position of the sporophore is likewise variable, usually arising on the rachis between the first and second pinna pairs, but sometimes above the second pinna pair. One unusual specimen possesses a sporophore at the normal place on the rachis plus secondary sporophores on each of the basal costae at the corresponding position between first and second pinnule pairs (Yunnan, *Yu 19897*). Rarely the sporophore arises between the bases of the two lowest pinnae, approximately as in *B. virginianum* (Fig. 3a). With such variability it is not suprising that a number of forms have been described as separate species. Even the level of ploidy varies. It is known to be tetraploid ($n=90$) and octoploid ($n=180$), and sterile hexaploids are known (Jermy & Walker 1977; Sahashi 1982).

Sahashi (1982) reported detailed observations on the habitat of *B. lanuginosum* in Nepal. He found that at lower elevations of 1000–2000 m, it is terrestrial, but at higher elevations of 2000+ m, many specimens are epiphytic on tree trunks or grow on moss-covered boulders. This is the only *Botrychium* that has been reported to be epiphytic. No specimens have been recorded as epiphytes in China. Various notations have been made on our specimens, such as open woods, rocky soil, shaded forest floor, and disturbed areas. The plants grow on the Yunnan–Guizhou Plateau (Fig. 1) at elevations of 1600–2600 m. Average January temperatures in that area are 12–14° C and July temperatures 28–29° C. Rainfall is roughly 400–500 mm in the eastern Qing-Zang Plateau and 900–1000 mm in the Yunnan–Guizhou Plateau.

Ching interpreted his new species *B. yunnanense* to be intermediate between *B. virginianum* and *B. lanuginosum* because of the cutting and position of the fertile segment just a short distance from the bases of the lowest pinnae. However, to us it appears to be just one of many forms of *B. lanuginosum*. *Botrychium parvum* is just a small form of *B. lanuginosum*. Such low-stature plants are commonly found growing together with large ones, and may simply be fertile juveniles which are well known in other species of *Botrychium*. The type specimen of *B. parvum* looks odd partly because the sterile segments and the sporophore are still somewhat immature and not fully developed. *Botrychium decurrens* is based upon a single and imperfect leaf with coarse cutting, and the normal wings along the upper rachis and costae are somewhat exaggerated. The specimen is abnormal, probably badly damaged when found, and possesses only one pinna, which the author of the species evidently confused with a whole blade. *Botrychium modestum* was an individual specimen separated from *B. lanuginosum* because of its small size, narrow and remote upper pinnae, and other characters known to be highly fluctuating. All of these presumed species are well within the expected morphological variability of *B. lanuginosum*. In the future it may be shown that there are specifically distinct elements within *B. lanuginosum*, but this can be justified only on the basis of extensive and critical field studies and collections. Highly variable species are well known in the genus, such as the widespread *B. simplex* and the eastern North American *B.*

dissectum. No other Chinese species of grapefern is as variable as *B. lanuginosum*.

5. *Botrychium virginianum* (L.) Sw., J. Bot. (Schrader) 1800(2):111. 1802.–*Botrypus virginianus* (L.) Holub; C. Y. Wu, Fl. Xizang. 1:34. 1983.

Botrypus tibeticus Ching in C.Y. Wu, Fl. Xizang. 1:34. 1983.–TYPE: Xizang (Tibet); Lingzhi, *Chinese Medicine Plant Invest. Team 3390* (PE!).

Illustration: Inst. Bot. (1974, p. 31).

Representative Specimens: **Shanxi** (1). Nanwutai Mt., *Y. T. Sphien 2025* (PE). **Sichuan** (2). Fu Mt., *E. H. Wilson 1033* (PE). **Yunnan** (4). Weixi, Zhang River, *K. M. Feng 3895, 4391* (both PE). **Hubei** (3). Qing County, Wudong Mt., *H. C. Chow 2530* (PE). **Xizang (Tibet)** (3). Salwin Kiukiang Divide, *G. Forrest 21659* (PE).

This very widespread and familiar circumboreal grapefern is apparently frequent in two main areas in China. It does not intergrade with its nearest relatives, *B. lanuginosum* and *B. strictum*. In Latin America and Antilles, however, *B. virginianum* intergrades with the plant commonly identified as *B. cicutarium* (Savigny) Sw. The type of *Botrypus tibetica* Ching is merely a very large form of *B. virginianum*. An additional specimen labeled "*B. laciniatum* Ching and Kung n. sp." was evidently not published and was later annotated as *B. virginianum*.

One wonders whether the similar species *B. lanuginosum* and *B. strictum* were not confused by Chinese doctors with *B. virginianum*, as these are often confused even by professional botanists. According to Ching (1959) the whole plant of *B. virginianum* is used as a source of medicine. It is purported to give relief from poisons, strengthen sexual ability, and aid in recovery from injury, especially by snake bite (Inst. Bot., 1974). This species was cultivated in a Chinese medicinal plant farm in Xinshan County, Hubei Province (Ching, 1959), and, we would assume, was grown elsewhere in the country.

The range of *B. virginianum* (Fig. 1) is roughly the same as the much less common *B. robustum* (see below). The two species appear in two places separated by the Sichuan Basin, namely Hubei and the Tibetan Regions. *Botrychium virginianum* occurs in valleys to upper mountain slopes and is capable of tolerating shade.

6. *Botrychium strictum* L. Underw., Bull. Torrey. Bot. Club 20:52. 1902.–*Osmundopteris stricta* (L. Underw.) Nishida, J. Jap. Bot. 27:276. 1952.–*Botrypus strictus* (L. Underw.) Holub; Shing, Glossary terms and names ferns 37. 1982.

Illustration: Tagawa (1959, p. 44).

Representative Specimens: **Jilin**(6). Antu County, Naitou Mts., *T. N. Liou 4253* (PE). **Liaoning** (1). Benqi, Dongyingshi, *Y. C. Zhu et al. 1321* (SFP). **Hubei** (1). Shennongjia, *Sino-Amer. Exped. 1686* (A/GH).

Misidentified as *B. virginianum* by many authors in the past, this species can be readily distinguished from it by characters of the sporophore and the trophophore. Although undoubtedly different from it, *B. strictum* resembles the Central and South American *B. virginianum* var. *mexicanum* (= *B. cicutarium*)

more closely in certain characters than it does B. virginianum. These include the shorter and simpler sporophore, the less divided pinnae, and the more winged costae and costules. As noted above, *B. cicutarium* intergrades and appears to be confluent with *B. virginianum*, and should probably be merged with it.

The whole plant of *B. strictum* is used as medicine for relief from poisons, and for recovery from snake bite injury (Inst. Bot., 1974).

The range was reported as extending to Shanxi and Yunnan by Ching (1959), but all but one of the specimens from China that we have examined are from Jilin, in Changbai Mountains. One specimen from Harvard University was collected in Hubei. The plants occur on the forest floor at elevations of 600 to 1100 m. The species occurs much further north than *B. virginianum*, but is very rare or absent from the Tibetan region of southwestern China.

7. *Botrychium japonicum* (Prantl) L. Underw., Bull. Torrey. Bot. Club 25:538. 1898.–*Botrychium daucifolium* var. *japonicum* Prantl, Jahrb. Königl. Bot. Gart. Berlin 3:340. 1885.–*Sceptridium japonicum* (Prantl) Lyon, Bot. Gaz. (Crawfordsville) 40:457. 1905.

Illustration: Sahashi (1983, p. 243).

Representative Specimens: **Jiangsu**(1). Jurong, Mopan Mt., *M. B. Deng et al. 3669* (PE). **Zhejiang**(1). Xi Tianmu Mt., *H. Migo s. n.* (PE). **Fujian**(1). without locality, *O. O. Chang 964* (PE). **Taiwan**(2). Taitotyo, Sinkogun, Kusuhara, *T. Suzuki 19618* (MICH). **Guangdong**(5). Ruyuan, *S. P. Ko 53622* (PE). **Guizhou**(3). Fanjing Mt., *C. P. Jian et al. 32464* (PE).

This species, which is very common and widespread in Japan from northern Honshu southward, has been reported only a few times from China. Poor specimens can be confused with *B. formosanum* and to a lesser extent with *B. daucifolium*. As might be expected from their respective overall distributions, in China *B. japonicum* occurs considerably to the north of *B. formosanum* and *B. daucifolium* (Fig. 1). *Botrychium japonicum* is recorded in swamps and wet woods, as well as along streams in valleys and along roadsides. Except for preferring damp sites, the general characters of the zones in which *B. japonicum* occurs are likely those of *B. ternatum*, a much more common species.

8. *Botrychium daucifolium* Wallich ex Hook. et Grev. Icon. fil. 161. 1829.–*Sceptridium daucifolium* (Wallich ex Hook. et Grev.) Lyon; Shing, Glossary terms and names ferns 37. 1982.

Botrychium subcarnosum Wallich ex Beddome, Ferns S. India 23, fig. 68, 1863.

Illustrations: Beddome (1892, p. 470); Sahashi (1981, p. 344).

Representative Specimens: **Yunnan** (4). Malipo, Laojun Mt., *K. M. Feng 13771* (PE). **Gwangxi** (1). Yao Mts., *C. Wang 40529* (PE). **Jiangxi** (1). Anyun, Jiagang, *J. F. Cheng 40248* (PE). **Taiwan** (1). Taito, near Zyonoru, Taito-gun, *M. Tagawa 1918* (MICH).

The group of *B. daucifolium*, *B. formosanum*, and *B. japonicum* (as well as *B. javanicum* Sahashi) involves closely related and variable taxa with distinctive but overlapping geographical ranges. Poorly developed or sterile specimens are often difficult to identify. We greatly need more and better specimens of these taxa. *Botrychium formosanum* appears to be somewhat intermediate between *B. daucifolium* and *B. japonicum*. *Botrychium daucifolium* is especially well

developed in India and Ceylon, ranging eastern and southward to Taiwan and the Malay Peninsula. Specimens are easily confused with *B. formosanum*, however, and some locality data may be erroneous. From *B. japonicum*, *B. daucifolium* differs not only in range, but in its less divided blades with the distal segments more adnate, the pinna apices more attenuated and pointed, and the tendency of the fertile stalk attachment to be higher, the common stalk extending usually to the distal half of the distance between leaf base and the base of the trophophore. The chromosomes of *B. daucifolium* number $n = 90$; those of *B. japonicum* $n = 135$. The latter number is rare among botrychiums, and is interpreted as a hexaploid based on $x = 45$.

Botrychium daucifolium grows in the Nanlin Mountain region and in northern Taiwan (Fig. 1), at elevations from 600 to 1900 m. The mean annual temperature of 20–22° C averages more tropical than that of *B. japonicum* at 16–21° C. The difference is more pronounced in winter: 12–14 vs. 5–12° C. Judging from label data, *B. daucifolium* prefers rich and moist sites in valleys, slopes, streamsides, and bamboo groves.

9. *Botrychium formosanum* Tagawa, Acta. Phytotax. Geobot. 9:87. 1940.– *Botrychium daucifolium* Wallich ex Hook. et Grev., sensu DeVol et al. Fl. Taiwan. 1:64. 1975.

Illustration: Sahashi (1981, p. 344).

Representative Specimens: **Guizhou** (1). Changfeng, *Y. Tsiang 43345* (PE). **Gwangdong** (2). Suni, *Y. K. Wang 31141* (PE). **Gwangxi** (1). Yao Mts., *C. Wang 40782* (PE). **Jiangxi** (1). Jiulian Mt., *Z. B. Yang 2424* (PE). **Yunnan** (1). Maguan, Gulingjing, *S. K. Wu 4166* (PE).

We have accepted the identification of these specimens on the authority of N. Sahashi. He wrote (1982, p. 123) that "This species differs from *S. daucifolium* . . . in having the blade inserted below the middle of the plant with the longer stalk, in the finer cutting of the blade and in the thinner texture." In the past this taxon was confused with both *B. daucifolium* and *B. japonicum*, between which, in some attributes, it is intermediate, as was first noticed by Tagawa (1940). The range of *B. formosanum* is especially interesting in this respect, for *B. daucifolium* runs from India and Ceylon to southern China to the Malay Peninsula to Taiwan; *B. formosanum* from southern China and Taiwan and north along the Ryukyus to the southern tip of Kyushu; and *B. japonicum* from eastern China and Taiwan, skipping most of the Ryukyus, and then extending through much of Japan, except for Hokkaido (Sahashi 1982, p. 164). We suggest that for further studies of this complex, efforts should be made in eastern China, including Taiwan, to locate mixed populations, in which two or three of the species grow together. The distinguishing characters could thus be studied in detail (Wagner & Wagner 1983). It seems probable that in Taiwan all three species may be found together. *Botrychium formosanum* is tetraploid with $n = 90$, like *B. daucifolium*.

The habitat of *B. formosanum is probably very similar to that of B. daucifolium*. In range, *B. formosanum* (Fig. 1) is evidently similar to that of *B. daucifolium*, but does not extend nearly so far to the west and north.

10. *Botrychium nipponicum* Makino, J. Jap. Bot. 1:5. 1916.

Illustration: Fig. 3b.

Collections Examined: **Guangxi.** Damiao Mts., *S. O. Chen 15395* and *16931* (both PE).

Evidently this species is very rare and local in China, being known at present only in Guangxi Province (Fig. 1). It was not recognized as a species, nor even cited, by Clausen (1938). Our specimens were identified as *B. nipponicum* var. *nipponicum* by Sahashi. He has listed numerous localities in Japan (Sahashi 1982, pp. 192–194, pl. 174). He also records it from near Seoul, Korea. The collections above are the first reports for China. It grows in moist sites in forest in valleys along slopes. The frond shape is very distinctive; the pinna tips are undivided and prolonged, and greatly resemble those of the eastern North American *B. dissectum* f. *obliquum*. As Sahashi has pointed out, the blades turn reddish in the winter.

11. *Botrychium robustum* (Rupr.) L. Underw., Bull. Torr. Bot. Club 30:51. 1903.–*Sceptridium robustum* (Rupr.) Ching in Shing, Glossary terms and names ferns 90. 1982.

Botrychium longipedunculatum Ching, Fl. Reipubl. Pop. Sin. 2:330. 1959.–*Sceptridium longipedunculatum* (Ching) Ching in Shing, Glossary terms and names ferns 90. 1982.–TYPE: Yunnan, Kunming, *Ducloux 14* (PE!).

Botrychium sutchuanense Ching, Fl. Reipubl. Pop. Sin. 2:330. 1959.–*Sceptridium sutchuanense* (Ching) Ching in Shing, Glossary terms and names ferns 90. 1982.–ISOTYPE: Sichuan, Chenkou, *Farges s.n.* (PE!).

Botrychium officinale Ching, Fl. Reipubl. Pop. Sin. 2:330. 1959.–*Sceptridium officinale* (Ching) Ching in Shing, Glossary terms and names ferns 90. 1982.–PARATYPES: Sichuan, Nanchuan, Jingfu Shan, *C. Pei 7299* and *W. P. Fang 938* (Both PE!).

Illustration: Fig. 3c.

Representative Specimens: **Sichuan** (5). Danba, Mochige, *The 8th team of forest management 2550* (PE). **Yunnan** (7). Chienchuan Mekong Divide, *G. Forrest 22546* (PE). **Liaoning** (1). Andong, *K. Kitsukin 8268* (PE).

According to Ching (1959), *B. multifidum* had recently been found in northeast China, but no specimens were cited. As we interpret it, *B. robustum* occurs in eastern Russia, Kamchatka, northern Japan and China (south to 33° N), and the Aleutians, but true *B. multifidum* occurs widely in northern North America and northwestern Eurasia. In equivalent large fronds, *B. robustum* is more divided than *B. multifidum* (3–4-pinnate vs. 2–3 pinnate), the segments are more overlapping (vs. more remote), more angular (vs. rounded or shallowly round-lobed), more lanceolate (vs. more oval), with margins more coarsely toothed (vs. entire or finely and shallowly denticulate or crenulate), the tips more pointed (vs. rounded to truncate), the veins in dried material are more obvious (vs. immersed), and the laminar surfaces somewhat rugulose with parallel elongate depressions (vs. plane). (Sahashi and Wagner are currently completing a detailed study of the relationships of *B. robustum* and *B. multifidum*.)

Botrychium longipedunculatum is apparently a compact sun form of *B. robustum* with an unusually large and well developed sporophore (as is common in exposed forms of practically all Botrychiums). The type specimen grew on a grassy slope. The other specimen so identified by Ching was found in a grassland. *Botrychium officinale* Ching specimens are more lax and have larger, less overlapping segments. The two habitats given are roadside and under forest. At best, this is a minor form of *B. robustum*. *Botrychium sutchuanense* Ching is a form similar to *B. longipedunculatum*, dwarfed with segments somewhat overlapping, presumably due to growth in an exposed habitat.

Botrychium robustum extends from the Qingling Mountains to the Chang Jiang River into the valleys southeast of the Qing-Zang Plateau (Fig. 1), from 800–4000 m, with an annual precipitation of 600–1000 mm. It occurs in disturbed areas, roadside, grassy slopes, and among shrubs. It is used as a medicine in China, providing relief from injuries (Ching, 1959). The name "*B. officinale*" as adopted by Ching probably referred to the medicinal uses of this plant.

12. *Botrychium ternatum* (Thunb.) Sw., J. Bot. (Schrader) 1800(2): 111. 1802.–*Sceptridium ternatum* (Thunb.) Lyon, Bot. Gaz. (Crawfordsville) 40:458. 1905.

Illustrations: Ching (1959, p. 17); Inst. Bot. (1974, p. 33).

Representative Specimens: **Anhwei** (1). Lantien, *D. Tsoon 2265* (PE). **Jiangsu** (2). Jingtan, Mao Shan, *M. B. Deng et al. 3618* (PE). **Zhejiang** (1). Mogan Shan, *Z. P. Jian et al. 61344* (PE). **Fujian**(1). Saxian, Lianhuafeng, *Y. Ling 667* (PE). **Jiangxi**(10). Pingxiang, Wenjiapo, *Jiangxi team 2586* (PE). **Hunan**(2). Huayun, *L. H. Liu 10093* (PE). **Hubei**(1). without locality, *P. C. Silvestri 3455* (PE). **Guangxi**(1). Zhuang divide, *S. H. Zhou 12522* (PE). **Sichuan**(2). Muchuan, *Sichuan economical plant team 2147* (PE). **Guizhow**(9). Chengfeng, *Y. Tsiang 4447* (PE). **Liaoning**(1). Xiuyan, Tangchi, *W. Wang 1457* (SPF). **Guangdong**(1). Lohfan Shan, *E. D. Merrill 11018* (US).

This common and widespread eastern Asiatic species is ordinarily quite readily distinguished from *B. robustum* because of its thinner, often delicately herbaceous texture, long-stalked pinnae, more strongly pointed, separated pinnules, and sharply denticulate margins. *Botrychium robustum* is generally more leathery, has pinnae with shorter stalks, coarser, more parallel-sided, and commonly approximate to overlapping segments. However, compact sun forms of the two species may be rather similar. The most distinctive form of *B. ternatum* grows in damp, deeply shady, grassy woods, and has extremely long, narrow trophophore and sporophore stalks and attenuated petiolules. The name *ternatum* has at one time or another been applied to practically all of the Chinese evergreen grapeferns.

Although it may be found in dry, open sites, *B. ternatum* is more commonly found on moist floors of dense forest and disturbed woods and frequently in bamboo groves. It commonly grows with or near *B. japonicum*. Its wide range is shown in Figure 1.

Botrychium ternatum is used as a medicine in China. It relieves poisoning and is used as a treatment for coughs and to stop bleeding (Inst. Bot., 1974).

Acknowledgments

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Literature Cited

Beddome, R. H. 1892. *Handbook to the ferns of British India, Ceylon and the Malay Peninsula.* London: W. Thacker.

Chen, S. P. et al. 1986. *Atlas of geo-science analyses of Landsat imagery in China.* Beijing: Science Press.

Ching, R. C. 1959. *Flora Reipublicae Popularis Sinicae.* Vol. 2. Beijing: Science Press.

Clausen, R. T. 1938. A monograph of the Ophioglossaceae. Mem. Torrey Bot. Club 19(2):1–177.

DeVol, C. E. 1975. Ophioglossaceae. In T. S. Liu et al. (eds.), *Flora of Taiwan.* Vol. 1. Taipei: Epoch Publishing Co.

_____. 1945. Ferns and fern allies of east central China. Mus. Heude Notes Bot. Chin. 7:1-154 + 4 maps.

Inst. Bot. Acad. Sin. et al. 1974. *Flora Tsinlingensis.* Vol. 2. Pteridophyta. Beijing: Science Press.

Jermy, A. C. and T. G. Walker. 1977. A note on the cytology of *Botrychium lanuginosum* and the occurrence of the genus in Malesia. Gard. Bull. Straits Settlem. 30:293.

Sahashi, N. 1978. Morphological and taxonomical studies on Ophioglossales in Japan and the adjacent regions (1). *Botrychium boreale* from Hokkaido. J. Jap. Bot. 53:51–60.

_____. 1981. Morphological and taxonomical studies on Ophioglossales in Japan and adjacent regions (6). Examination of *Sceptridium daucifolium* (1). J. Jap. Bot. 56:339–347.

_____. 1982. Morphological and taxonomical studies on the Botrychiaceae in Japan and the adjacent regions. Ph.D. dissertation. Toho University, Japan.

_____. 1983. Morphological and taxonomical studies on Ophioglossales in Japan and the adjacent regions (8). New taxa of *Sceptridium* in Isl. Oshima, the Izu Islands. J. Jap. Bot. 58:241–247.

Tagawa, M. 1940. Studies on Formosan ferns. 1. Acta Phytotax. Geobot. 9:87–96.

_____. 1959. *Coloured Illustrations of the Japanese Pteridophyta.* Osaka, Japan: Hoikusha Publishing Co.

Wagner, W. H. Jr. and F. S. Wagner. 1983. Genus communities as a systematic tool in the study of New World *Botrychium* (Ophioglossaceae). Taxon. 32:51-61.

Wu, C. Y. et al. 1980. *Vegetation of China.* Beijing: Science Press.

_____. 1983. *Flora Xizangica,* Vol. I. Beijing: Science Press.

SHORTER NOTE

A Disjunct Station of *Asplenium ruta-muraria*, with *Pellaea atropurpurea* and *P. glabella*, in Eastern Ontario.—In March 1988, I observed about 200 plants of *Asplenium ruta-muraria* L. growing along 800 m of west-facing conglomerate rock on the east side of the Rocky Narrows, about 1.5 m above the highwater mark of Big Rideau Lake, South Burgess Twp., Leeds Co., Ontario (*Munro 3110*, DAO). These plants grew from 0.5 m to 4.5 m above the highwater mark. I also found about 200 plants of *Pellaea glabella* Mett. ex Kuhn var. *glabella* along about 100 m of this same cliff, growing from 0.3 m to 5 m above the highwater mark (*Munro 3111*, DAO), and about 50 plants of *Pellaea atropurpurea* (L.) Link on the cliffs and on thin grass slopes at the southern end of this location. These plants were growing from 3 m to 12 m above the highwater mark (*Munro 3112*, DAO). In June, two sites with an additional 250 plants of *Pellaea glabella* were found 4.5 km and 5.5 km south along the lake on two islands (*Munro 3114, 3115*).

Wall-rue, *Asplenium ruta-muraria*, occurs through parts of east and central North America including Ontario, Quebec, and Vermont, south through New York and Pennsylvania to Alabama and Mississippi and west to Arkansas and Missouri (Lellinger, *A field manual of the ferns & fern-allies of the United States & Canada*, 1985). There are also disjunct populations in northern Michigan in Chippewa and Keweenaw Counties (Billington, *Ferns of Michigan*, Bull. 32, 1952). In Canada, *A. ruta-muraria* has been known from only two localities in Ontario, namely Manitoulin Island and the northern end of the Bruce Peninsula, Bruce County. Both locations are in the northern Lake Huron region (Soper, Amer. Fern J. 45:97–104, 1955; Dickson & White in Argus & White, eds., *Atlas of the rare vascular plants of Ontario*, Part II, 1983). *Asplenium ruta-muraria* is also found in Quebec along Baie Missisquoi, the northeastern part of Lake Champlain. This plant is considered rare for Canada (Argus & White, *The rare vascular plants of Ontario*, Syllogeus No. 14, 1977; Bouchard et al., *The rare vascular plants of Quebec*, Syllogeus No. 42, 1983).

This new station represents a significant disjunct range for *A. ruta-muraria*, being 230 km west, 375 km east and 195 km north of previously known sites. A recent map of the Canadian distribution is given in Cody and Britton (*Ferns and fern allies of Canada*, in press). *Asplenium ruta-muraria* is a calciphilous fern which is commonly epipetric on dolomitic limestone rock.

Purple cliff-brake, *Pellaea atropurpurea*, is wide-ranging in North America from British Columbia to Quebec, Vermont and Rhode Island, south to Florida and west to Wyoming, Colorado, and Arizona (A. Tryon, Rhodora 74:220–241, 1972). In Canada, several sites are known from southeastern British Columbia, adjacent Alberta (Brunton, Canad. Field-Naturalist 93:288–295, 1979). It is also found as an outlier along Lake Athabasca, Saskatchewan, in Ontario on Manitoulin Island and the northern Bruce Peninsula, Niagara Falls, eastern Ontario and western Quebec, and in Montmorency Co., Quebec (Rigby & Britton, Canad. Field-Naturalist 84:137–144, 1970; Brunton & Lafontaine, Naturaliste.

Canad. 101:937–939, 1974; Cody, *Ferns of the Ottawa District*, 1978; Dickson & White, 1983). This fern is classed as rare in Canada by Dickson and White (1983).

Smooth clif-brake, *Pellaea glabella*, occurs through parts of east and central North America including Minnesota, Ontario, Quebec, Vermont then south to the mountains of Virginia and Tennessee and southwest through Arkansas to northern Texas (Lellinger, 1985). In Canada, this fern occurs sporadically along the entire length of the Niagara Escarpment in Ontario to Manitoulin Island with a few locations in northwestern Ontario and eastern Ontario. There are only two geographical locations known for var. *glabella* in Quebec. These are in Gatineau and Richmond counties (Rigby & Britton, 1970; Brunton & Lafontaine, 1974; Cody, 1978). This variety of *Pellaea glabella* is considered rare in Canada (Argus & White, 1977).

The two *Pellaea* spp. are comparatively more common in eastern Ontario but the nearest known stations are about 50 km away in several directions for either species. Recent maps of the Canadian distribution of *P. atropurpurea* are given in Cody and Britton (in press). Maps of the distribution of *P. glabella* for Canada and Ontario are found in Cody and Britton (in press) and Brunton and Lafontaine (1974). Both species are calciphilous. At this locality, *P. atropurpurea* plants receive at least partial shading from trees or shrubs. On the higher cliff-face plants of this taxon grew intimately with *A. ruta-muraria* along several seams. *Pellaea atropurpurea* exhibited a large and open growth pattern while *P. glabella* grew in fasciculated clusters. *Pellaea glabella* was found on the more exposed and probably drier poriton of the conglomerate rock. Along one crack in the rock, plants of both this taxon and *A. ruta-muraria* were growing intimately together.

This Big Rideau Lake site is unusual because of the conglomerate rock substrate. The nearby rock stratum is Grenville crystalline limestone and quartz with belts of rusty weathered gneiss (Wilson & Dugas, *Geology of Perth Map Area*, Map 1089A, 1961). This poorly sorted boulder conglomerate may represent the base of the Nepean Formation which is Cambrian in age. The conglomerate probably constitutes an anomalous thick section and it lies unconformably on crystalline Precambrian rock and is derived from the same. The pebbles and boulders are mostly rounded marble with angular fragments of quartz, marble and granite pegmatite minerals cemented into the loose matrix. Cleavages of calcite crystals are also present and are indicative of quick reburial with little chemical action and weathering. This conglomerate cliff lies within 100 m of a fault-line and probably represents an eroded fault-line scarp (pers. comm., Gary Ansell, Geological Survey of Canada, Ottawa). An application of 15% HCl produced vigorous bubbling, indicative of carbonate. The pH of the rooting medium was measured from two substrate samples at 6.9 and 7.1. This cliff faces west and would be in the afternoon sun for several hours in the summer. However, many of the ferns were either growing in the shade of overhanging trees or occurred in cracks where white calcium deposits could be seen, evidently from seepage. The loose structure of the conglomerate provides an ephemeral habitat for the ferns. As noted above some plants grew within

0.3 m of the highwater mark and would be washed by wave action on windy days.

The dominant tree species were *Pinus strobus*, *Thuja occidentalis* with many *Juniperus virginiana*. Other woody plants included *Arctostaphylos uva-ursi*, *Betula papyrifera*, *Fagus grandifolia*, *Juniperus communis*, *Lonicera dioica*, *Pinus resinosa*, *Ribes sp.*, *Sambucus pubens*, *Shepherdia canadensis*, *Symphoricarpos albus*, *Tilia americana*, *Tsuga canadensis*. The forbs included *Aquilegia canadensis*, *Carex eburnea*, *Linaria vulgaris*, *Minuartia michauxii*, *Oryzopsis asperifolia*, *Pedicularis canadensis*, *Poa compressa*, *Polygonatum pubescens*, *Saxifraga virginiensis*, and *Viola adunca*. Other ferns growing above the cliff face included *Cystopteris fragilis* s. lat., *Dryopteris marginalis*, and *Polypodium virginianum*. This locality represents an interesting range extension for these three fern species. Interpretation of the local geology maps suggests that further locations may be found for these rare ferns. This station is located on private land but the conglomerate cliff will probably prevent extensive human damage to the plants.

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